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ABSTRACT

Parasites and related symbionts of marine and estuarine hosts of the northern Gulf of Mexico are described in this guidebook. It is meant primarily to serve as a teaching aid for the novice student, but it also contains more technical aspects for the experienced parasitologist. Forms and examples of symbiosis are explained in an introductory statement. Information, diagrams, and illustrations on the various hosts of parasites are then presented in separate sections. These include: (1) invertebrates as hosts (highlighting symbionts of the American oyster; blue crab, penaeid and grass shrimp); (2) vertebrates as hosts (concentrating on parasites of fishes, the alligator, birds, and marine mammals); (3) miscellaneous symbionts (explaining the infestations by selected nematodes, flatworms, barnacles, and gnats); (4) fish-kills and miscellaneous diseases (identifying causal factors contributing to the kills); and (5) technical aspects (citing research findings related to the specific organisms covered in preceding sections). A listing is provided of all the referenced literature and a glossary is also included of the common terms related to symbionts. (ML)

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MARINE MALADIES?
Worms, Germs, and Other Symbionts From the Northern Gulf of Mexico

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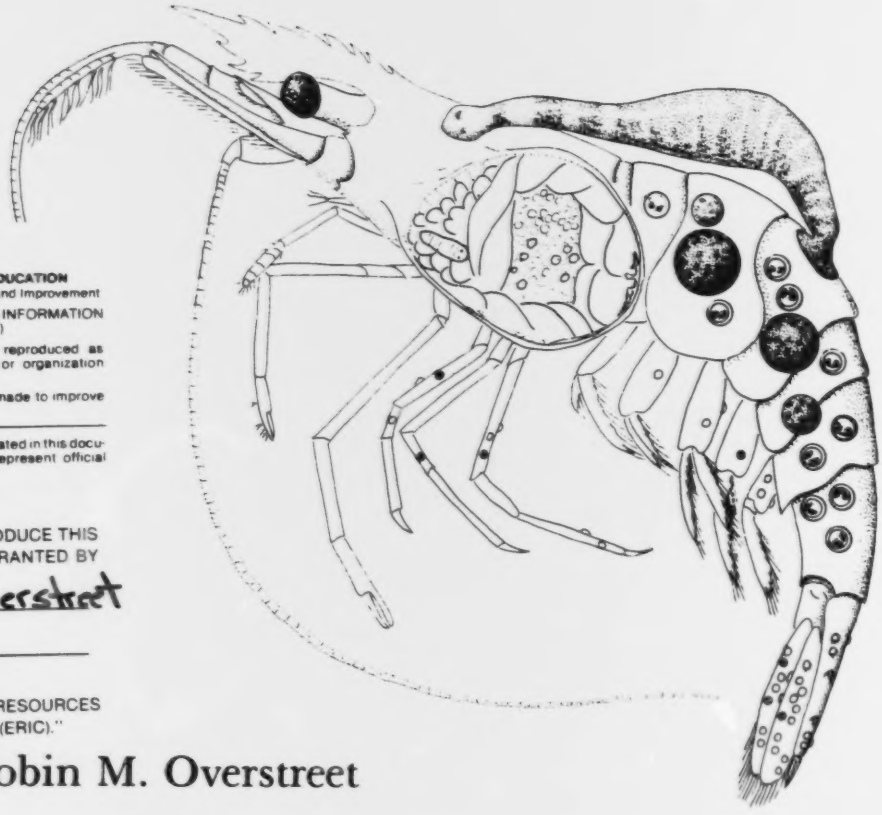

Robin M. Overstreet

MISSISSIPPI—ALABAMA
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MARINE MALADIES?
Worms, Germs, and Other Symbionts From the Northern Gulf of Mexico

by

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PREFACE

This guidebook will inform those curious about parasites and other symbionts associated with marine and estuarine hosts in the northern Gulf of Mexico. Designed as a teaching aid for students, fishermen, seafood consumers, beachcombers, and even parasitologists, it should allow for better understanding and appreciation of several of the numerous shellfish and finfish symbionts. (A symbiotic organism is one that interacts with the host in or on which it lives.) Even though most selected examples are from Mississippi and other regions along the northern Gulf, the same or related species also occur along the Atlantic seaboard and elsewhere; present information should apply similarly for several but not all of those cases. Some symbionts significantly affect the size and production of a fishery and consumption of the product, whereas others mostly stimulate environmental or academic interests. In the natural environment, parasitic relationships seldom result in harm to the host. Harm, however, often becomes apparent when animals are concentrated and confined as they are during culture or when they are otherwise stressed. This guide will discuss some of those cases.

This guidebook is divided into sections discussing the various hosts of parasites. Primary headings refer to basic host-types. The reader, however, must keep in mind that groups of both symbionts and hosts overlap. The same parasite may have a different stage of its life history infecting a shrimp, a fish, and a bird. Consequently, perusal of several sections may help the reader understand more about the symbionts of any particular host.

The guidebook has been written with both the student without a strong biological background and the layman in mind, but it presents additional separate notes for more serious readers interested in technical aspects. That technical section, in the latter half, directs the reader to referenced scientific literature which either presents supporting data or reviews the topics under consideration. An effort has been made to define scientific terminology either in the text or in a glossary at the end of the guide. Terms presented in the glossary are indicated by an asterisk (*) the first and occasionally other times they are used. Diagrams, illustrations, photographs, and legends provide further assistance.

Latin names have been included as well as common names for three reasons. First, some organisms have no common name. Second, a specific common name may refer to more than one animal or one animal may have several common names. When most people talk about *the* blue crab, they probably talk about *Callinectes sapidus*, but they might also knowingly or unknowingly be referring to *Callinectes similis*, *Callinectes ornatus*, or a variety of other related crabs. On the other hand, residents of Mississippi call the spotted seatrout *(Cynoscion nebulosus)* a speck or speckled trout whereas people elsewhere may call it or a related species by the name weakfish, squeteague, or any of several others. Third, knowing a Latin name often allows one to more easily find other literature about the organism.

A binomial name, that is the two-component Latinized name of an organism, consists of the capitalized generic name and the noncapitalized specific name. One or several species may occur in a genus, and different taxonomists, scientists who deal with the nomenclatural problems, may not all agree to which genus a given species belongs. Nevertheless, names allow people to refer to specific organisms. Some names reflect the animal's characteristics, its locality, or its finder, whereas others are merely fabricated.

Readers interested in the hygienic aspects of eating infected finfishes and shellfishes may be comforted by the fact that *cooking destroys all potentially harmful agents in seafood products from the northern Gulf of Mexico.* Perhaps this statement needs some qualification. A person could acquire gastric distress from eating cooked seafood if staphylococci toxin was present, if contam-

ination occurred after cooking, if the product was spoiled before cooking, or if condiments contained salmonellae, shigellae, or some other infectious bacteria. Also, heavy metals and some other nonparasitic toxins are not destroyed by cooking. Products infected with parasites should not dismay a consumer. Seldom does one get the opportunity to see some of these puzzling little invaders! If infected products are cooked, all become edible, a few have less appeal and flavor, and several taste better because of the added rich, juicy worm nestled among the tissue. I am willing to admit, however, that most people preferring infected products do not realize that the "flavor bud" is a parasite.

INTRODUCTION TO SYMBIOSIS

As is the case with many scientific endeavors, the same concept or item may be referred to by different terms, and, conversely, different concepts or items can be called the same name. Seldom does one realize that confusion exists until he progresses into a discussion. What is a parasite? Does it have to harm its host? If so, does it have to harm all the different hosts in all stages of its life? Does it have to be smaller than its host? Can it be the same species as the host? Depending on how one prefers to answer the above questions, even a human baby can qualify as a parasite. Before birth the fetus nourishes itself at the expense of its host (mother) and releases toxic wastes into that host; occasionally at birth, it even causes the host's death. After normal birth, it continues to suck vital nutrients from the host. From another viewpoint, even after maturing, that offspring may obtain its well being from its parents or friends at their expense. By defining terms now, we should have a clearer understanding of some of the different types of relationships among animals. Three terms that must be understood to aid in understanding parasites are "symbiosis," "commensalism," and "mutualism."

"Symbiosis," which means "living together," accounts for a variety of long and short term relationships that benefit one or both parties. For purposes of simplicity, I consider symbiotic relations to be those specialized associations ranging from commensalism, where neither party is harmed and both could live without the other, to mutualism, where both parties benefit each other and neither could live without the other. A true parasite lies in between. Parasitism defines a one-way relationship in which one partner, the parasite, depends upon and benefits from the other partner, the host. The host is usually the larger of any two associates and can be harmed by the parasite. Actually, much overlap in types of relationships exists, and, for most readers, what happens in a given relationship far surpasses in importance the term someone may want to tag on it.

"Commensalism" means "eating at the same table." A sea anemone attached to the molluscan shell of a hermit crab derives mobility and scraps of food from the crab without being metabolically dependent on it. The relationship, however, might not be one sided and may be truly mutual. In some cases, the anemone, by virtue of its stinging tentacles, contributes by warding off octopuses or other predators from the crab. The degree of benefit to each party depends on the species of anemone and crab involved as well as the environmental conditions and the additional organisms which make up the community*. In the northern Gulf of Mexico, a specific anemone *(Calliactis tricolor)* usually attaches to a shell, often of the moon snail, inhabited by a hermit crab *(e.g., Pagurus longicarpus)*, as illustrated in Figure 1.

Some inhabited shells harbor hydroids rather than anemones. Two species of hydroids *(Podocoryne selena* and *Hydractinia echinata)* commonly use this movable substratum* in the northern Gulf of Mexico (Figure 2). They probably benefit the crab because colonies of each possess protective

Figures 1 and 2. Hermit crabs with symbionts on their molluscan shells. Top, two individuals of an anemone (*Calliactis tricolor*) on the moon snail inhabited by *Pagurus longicarpus*. Bottom, a hydroid covering the shell housing *Pagurus pollicaris*.

stinging zooids* in addition to the nutritive, generative, and sensory ones found in colonies of related nonsymbiotic hydroids.

Commensalism can be expanded to include "phoresis" meaning "traveling together." The two parties in this relationship do not eat at the same table. A possible example of a phoront is a hydroid (*Clytia* sp.) that attaches to the posterior edge of a live coquina's shell (Figure 3). These clams in Texas with the hydroid attached contained no internal parasitic flukes. This finding suggests the hydroid prevented the parasitic infection*. If true, we could interpret the clam-hydroid relationship as mutualistic, a relationship to be discussed later, because both parties benefit. If *Clytia* sp. is a phoront, it benefits only by utilizing

Figure 3. A commensal hydroid (*Clytia* sp.) attached to a coquina clam (*Donax roemeri protracta*). The hydroid benefits by having a substratum along a sandy beach on which to attach, but neither clam nor hydroid harms the other.

the clam shell as something hard on which to attach in the turbulent beach habitat. If, however, the clam benefits by being protected from infection by a parasite that destroys its reproductive tissue, that hydroid is somewhat mutualistic even though both the clam and hydroid can live without the other.

Already the reader probably realizes that we do not always know what constitutes a parasite. When a symbiont depends entirely on a host, occasionally harming it in the process, it is unequivocally a parasite. Harm can result from boring into tissues, digesting tissues, displacing vital tissues, releasing toxic metabolic products, or competing for nutrients. Some parasites even live apart from their hosts for a portion of their lives, whereas others always remain with their hosts, but act as commensal until confronted with a particular stress. Tapeworms and spiny-headed worms are obvious parasites since they have no gut and necessarily depend on their hosts to provide all their nutrients in a state that can pass through their body surfaces. Whether many other symbionts are parasites requires a subjective decision.

The difference between a parasite and predator can also be confusing. Some animals kill their prey outright rather than depend on a living source of food, and these constitute predators. When animals feed on a variety of prey much smaller than themselves, they act as predators. However, some micropredators and even large predators periodically eat away part of specific species

of prey without killing them, and these could be considered parasites. I will let the reader term such a relationship anything he desires, but the more biochemically and physiologically dependent a "predator" becomes on a given "prey," the more parasitic the relationship becomes.

In a well-adapted host-parasite relationship, the host is not significantly harmed. This may sound like a contradiction, but as a parasite becomes more dependent on a specific host species, it becomes more vulnerable to extinction if it or anything else seriously harms that host. It must be able to obtain its well being from the host without harming it because the parasite needs a healthy host to survive. Strangely, however, a well-adapted parasite often benefits when one of its larval stages affects the intermediate host in such a manner that the final host can prey on that intermediate host more easily and thereby insure completion of the parasite's life cycle.

Usually for a parasite to harm its host, the host is either stressed or weakened or the infection is either "accidental" or heavy. An accidental, or incidental, parasite afflicts a host other than its normal one. Excessive numbers of an otherwise harmless parasite in the normal host can cause disease•. Twenty or so hookworms in an individual's intestine would have no esthetic appeal if he knew about them, but such an infection would not constitute disease. When the number of worms increases, especially in a malnourished patient, a disease becomes manifest. The actual number of worms needed to cause bloody stools, anemia, loss of appetite, a desire to eat soil, and other symptoms of disease depends on both the species of hookworm and the individual person (host) involved.

"Mutualism" requires that both mutuals depend on each other. In the strict sense, this must be a metabolic• dependency in which neither party survives without the other. The combination of a termite with its internal protozoans provides an example close to home. Intestinal flagellates produce the enzyme cellulase which digests the ingested wood so that the termite can utilize it. Neither animal can survive for long by itself, and the two together do much to benefit an ecological community• (assuming a house is not the food source!). In the ocean, numerous cases of mutualism occur. Many of these include specific algae associated with particular invertebrates.

Symbiotic algae inhabit various tissues or cells of invertebrates belonging to numerous genera in at least ten phyla•. Reef-building corals provide often-mentioned examples. An assumption dictates that all the invertebrate hosts would die without their algae, but experimental studies have shown that these otherwise greenish or brownish (from chlorophyll•) corals and other cnidarians may survive when bleached in darkness from shedding their symbionts. Nevertheless, the well-adapted relationships benefit both parties, even though some animals may appear to exploit their algal mutualist excessively. In each association, the benefits probably vary, and most have not been thoroughly investigated. The invertebrate host provides nutrients and shelter for the alga. The alga provides the host oxygen and organic nutrients (by photosynthesis•); removes carbon dioxide, nitrogenous wastes and other metabolic products from host cells; provides protective coloration for the host; and in the case of corals, aids in deposition of a calcified skeleton. Few of these algae have been cultured and properly identified. Consequently, for most associations, an alga's possible relationships with different invertebrates, its metabolic demands on a host, and its ability to live without a host have not been firmly established.

Most conspicuous examples of invertebrate-alga mutualism occur in tropical waters, but some less conspicuous ones occur in the northern Gulf. Perhaps some readers will search for the typically greenish or brownish invertebrate hosts. One is the sun jellyfish *(Cassiopea xamachana)* which occasionally can be found near Horn Island

where, when not swimming, it rests on the bottom with its underside facing up, exposing the algal symbionts.

Hosts from Florida which appear to utilize multiple symbionts are colonial zoanthid anthozoans (two species of *Zoanthus*, see Figure 4 for one of them). Their greenish-brown polyps with extruded tentacles give the impression of a flower; the color is derived mostly from the internal golden-brown zooxanthella. Rather than having one symbiont like corals and other investigated hosts, these cnidarians have a variety of symbionts. One form migrates extensively, perhaps depending on the amount of light present. Since the Floridian zoanthids readily feed when presented small crustaceans or pieces of fish, the symbionts appear to have a function other than a sole nutritive source. Some other animals culture their food. Algae are grown in amphipod tubes by some amphipod inhabitants, and fungi grow on the pieces of leaves provided by leaf-cutting ants. The identification and interrelationships among the zoanthids and symbionts other than the zooxanthella (alga) which is similar in appearance to that in most other cnidarian-algal associations have not been established.

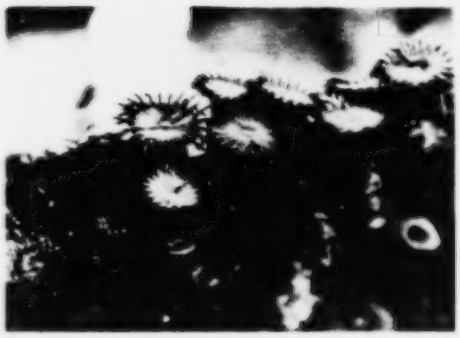


Figure 4. A colonial zoanthid anemone commonly called a green sea mat. The animal normally utilizes internal plant and animal symbionts for its well-being.

INVERTEBRATES AS HOSTS

THE AMERICAN OYSTER

The American oyster *(Crassostrea virginica)* supports an important fishery in most regions where it occurs along the Atlantic and Gulf of Mexico coasts from Canada to Mexico. The benthic* animal grows rapidly in the warm water of the northern Gulf, reaching 8 centimeters (cm) (about 3 inches, see glossary for examples of measurements) in as short a period as 4 months, but typically taking a year or so. When on soft mud, it sinks and consequently grows thin and long to keep its bill, or flared end, above the mud. On the other hand, on a firm uncrowded bottom, the oyster forms a broad cupped shell. It grows best in estuarine* water with reasonably constant salinity* between 15 and 30 ppt.

Figure 5 illustrates a partially shucked (opened) oyster. In a closed oyster, the two valves join anteriorly immediately internal to the umbo, or beak, by a continually replaced elastic hinge ligament. The large adductor muscle, referred to as the "eye" by shuckers, holds the valves together and must be cut to open the oyster.

Special cells in the mantle secrete three primary layers of the shell. Externally, a thin horny organic layer (periostracum) covers a middle prismatic layer of mineral which develops most substantially on the right flat valve. The inner shiny layer (calcitic ostracum) usually constitutes the thickest stratum.

Features of the soft body are mostly self-explanatory. Dark bands of sensory tentacles border mantle flaps. Ciliary rows of the gills direct up to 28 liters (about 30 quarts) of water per hour. The gills remove oxygen from and excrete wastes into that water. They also accumulate food which, when acceptable to the oyster, continues to be conveyed to the mouth by action of cilia (these structures will be described in a later section on protozoans of fishes) on the gills and palps.

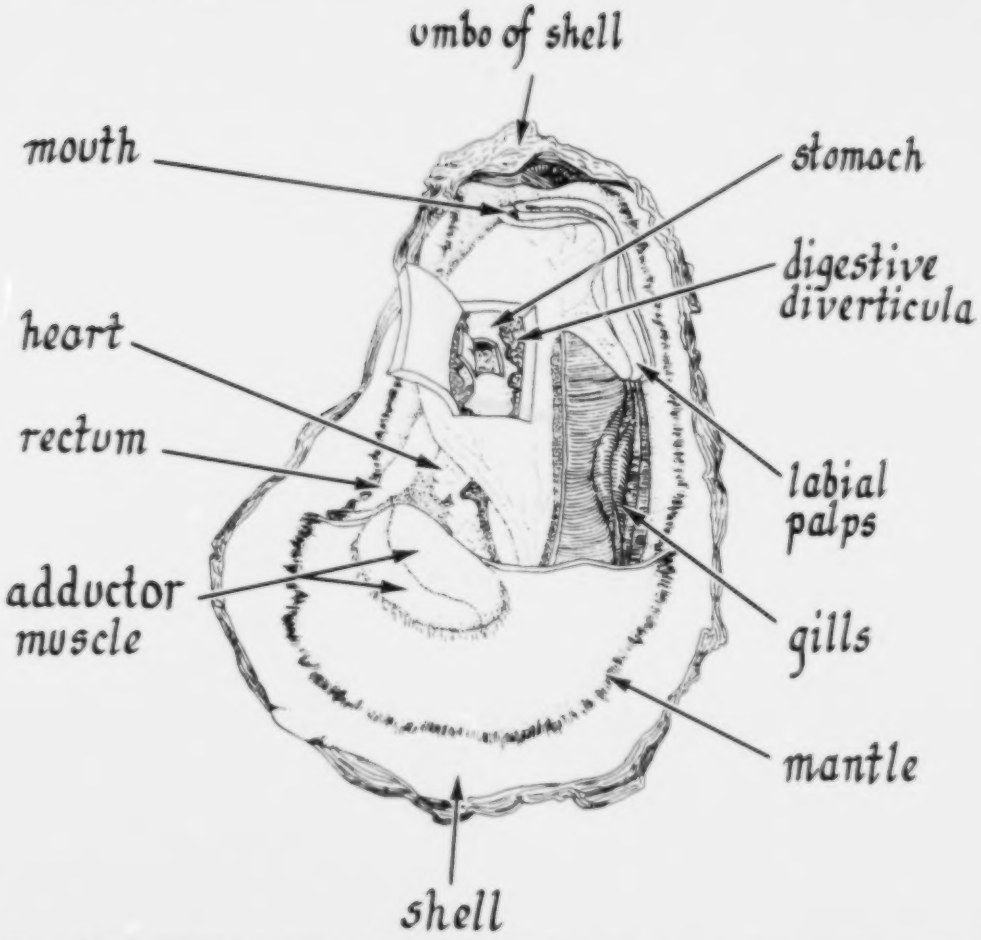


Figure 5. Selected anatomical features of the American oyster. One valve has been removed and portions of the oyster's soft tissues cut out to reveal structures.

Most young oysters function as males, but may change sex one or more times in subsequent years. During warm weather between April and October an individual's spawning often stimulates others to spawn. Each oyster releases millions of eggs every spawn and can spawn several times per season. After a larva develops, it settles in about a week and searches for a hard clean surface on which to cement itself. The greatest reproduction and subsequent "setting" of young oyster larvae occurs in May or June, depending on the water temperature. The small oysters, called spat, often set on larger oyster shells, but will utilize almost anything. All stages are vulnerable to some kind of symbiont. Predation is also typically heavy, especially in summer. Because of this predation, a greater number of young oysters from the fall set typically survives to the following year compared with the relatively larger spring set of spat.

Public Health Aspects

People may be concerned about the possibility of a parasitic infection from consuming raw oysters. No such parasite from the American oyster has been implicated in health problems. On the other hand, oysters from polluted water do concentrate pathogenic human viruses and bacteria. These human pathogens, however, are killed by proper cooking and usually are not present in oysters harvested from noncontaminated

Figure 6. The middle gaping oyster cannot close its valves tightly. Several disease-agents and environmental stresses can cause gaping, but this condition is a common sign during the hot summer indicating that the oysters may have heavy infections of dermo. These dying oysters become easy prey for a number of predators, including organisms previously acting as commensals.

waters. Certain inorganic contaminants, such as lead or mercury, and some algal toxins are sometimes found in polluted waters, and these may be concentrated in oysters growing there. These potential toxins are not removed by cooking.

Even though not harmful to man, several parasites do injure the oyster. Most of these cause significant disease* in oysters only when antagonized by additional stresses. Environmental stresses — such as high temperature, low salinity, excessive siltation, or pollutants — probably all affect some symbiotic relationships. When threatened, the soft-bodied oyster closes together its two thick shells, or valves. After becoming overpowered by predators or intolerable conditions, the oyster gapes (Figure 6) and soon after dies or is eaten.

Dermo

Many oysters in the northern Gulf of Mexico gape because of "dermo" a colloquial name for a disease caused by *Dermocystidium marinum* (presently known as *Perkinsus marinus*). This microorganism, once thought to be a protozoan, then a fungus, and now a protozoan again, cannot be seen without a microscope; however, oysters dying in late summer with a shrunken appearance and a yellowish cast probably have dermo. For a long time such *mortalities* in Louisiana had been blamed on oil pollution until the oil industry contracted Texas A&M to investigate the problem in the 1950's. Findings of that study revealed many things about the dermo organism, including how to detect it easily. When infected oyster tissue is placed for a week or more in a thioglycollate culture medium with antibiotics, the organisms enlarge and become readily distinguishable. These enlarged cells develop a wall which turns a bluish-black color when stained with an iodine solution (Lugol's) (Figure 7). Clusters of these spores* can be detected without a microscope. Most tissues of infected individuals harbor the parasite, but the gills, rectum, mantle, or adductor muscle provide the best results.

Infections* by dermo have important economic implications. The prevalence* (percentage) of infected oysters and the number of organisms per infected individual typically remain low during winter and increase considerably during summer. Periodically, the majority of adult oysters on a reef succumb to this pathogen during hot summer months, producing massive kills, or epizootics. In order to avoid the loss of these oysters to consumers several years ago, William Demoran of the Mississippi Marine Conservation Commission would sample oysters from

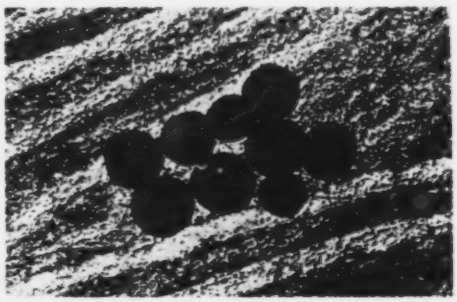


Figure 7. Enlarged spores of dermo (*Dermocystidium marinum*) that have been cultured in a special fluid (thioglycollate medium) and stained with iodine. The method allows easy detection of this organism which kills many stressed oysters during the hot summer.

Lower Square Handkerchief Reef during the winter. If the sample revealed a high prevalence of dermo, the Commission allowed most of the oysters from that vulnerable region to be harvested then, rather than wait for the expected summer mortalities.

Salinity has often been considered the critical factor regulating the disease since infections rarely occur in water less than 15 ppt. Such is not always the case. In fact, biologists from Mississippi and Florida have found over half of many samples from water less than 15 ppt to be infected. Often oysters have infections in water that is fresh or quite low in salt content.

Apparently temperature acts as the primary controlling factor. Acquisition of most infections probably occurs during a period of high salinity, but development is most pronounced when temperature is relatively high. High temperature may decrease the host's ability to defend itself against the organism, just as indiscriminant use of steroids can cure one condition in a person but allow another previously controlled condition to become expressed.

Juvenile oysters do not seem to develop dermo as readily or severely as older ones. Although host-mediated resistance• (also see humoral and cellular mechanisms in glossary) in juveniles has been suggested, the phenomenon is probably because young oysters are in comparatively better health than older ones and therefore better able to fight off or control any challenging infective agents. Active defense mechanisms used to fight the parasite are well known and chemical defenses may exist as well. Also, young oysters commonly grow so fast that they can reach adult size as fast as an infection can occur. This is especially true of the numerous late summer-spawned oysters that grow through the winter when the parasite is limited by lower temperature. Oysters seem most susceptible to infection and disease immediately after spawning. The extreme stress associated with spawning apparently greatly weakens the oysters and their defenses against the parasite.

Heavy oyster mortalities — an estimated 50% of the crop — occur annually on the average from the disease in Florida. Fortunately, spat and juveniles quickly reestablish reefs, even after extensive die-offs.

Dermocystidium marinum is considered rather specific for the American oyster. However, a few other invertebrates harbor similar and, in some cases, identical spores, but apparently do not undergo mass mortalities. Actually, several related, poorly-understood species infect oysters and other invertebrates, and some of these can cause mortalities in stressed hosts.

Other Symbionts and Diseases

Several other organisms in addition to dermo-like agents cause disease in oysters. Most necessitate a microscope to see. An unidentified "mycelial" (suspected fungus, see hypha in glossary) disease infects oysters from at least Texas and Louisiana primarily in spring; infections result in some mortalities, but show no obvious relationships with salinity.

Other diseases of bacterial and fungal origin also occur. One discussed here is "foot disease." That name is a misnomer because the oyster's foot, an organ which aids crawling of the larva before it attaches, becomes rapidly resorbed by the young spat after setting. Apparently caused by a fungus, small rough greenish spots speckle the inside of the shell under the attachment of the adductor muscle. In severe cases, part of the muscle separates from the shell and a horny elastic cyst forms. As it extends beyond the site of attachment, the cyst acquires a hard calcareous encasement. The site of attachment necessarily changes continually to accommodate growth of the oyster and shell. Thought by some to be more prevalent in warm muddy waters, foot disease makes an oyster vulnerable to predation because the valves no longer close efficiently.

The cyst illustrated in Figure 8 may be foot disease, a rare condition in Mississippi

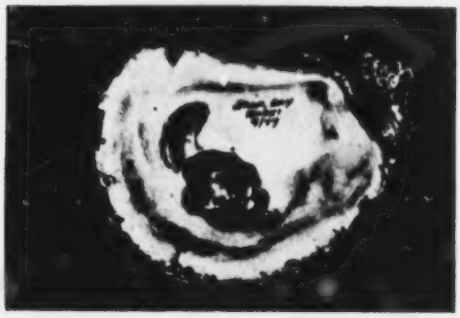


Figure 8. A hard horny growth secreted by the oyster. This may exemplify "foot disease," a reaction by the oyster against a fungus under the attachment of the adductor muscle. Low quality pearls form when the oyster secretes a protective coating around an irritant.

Sound, or some other similar condition. A variety of hard growths can develop in an oyster. Pearls form when the oyster secretes a protective calcareous coating around an irritant such as a sand grain or a larval parasite, but these rarely have the quality essential for good jewelry. "Mud pearls" may also be caused by penetration of mud worms at the site where the adductor muscle attaches.

Consumers occasionally worry about eating pink oysters. This condition typically develops in oysters refrigerated for a few days. A yeast can cause this, and it is destroyed with even minimal cooking. Other discolorations occur in live oysters. The adductor muscle of an oyster that has fed on a specific diatom (a very small alga) "bleeds" a reddish pigment when cut. Certain dinoflagellates (other small algal forms) and heavy metals also cause discoloration in various tissues.

A microscope allows detection of spores• of a gregarine protozoan. Two similar species, one infecting mostly mantle tissue and the other infecting gill tissue, occur commonly in Mississippi. Within the spores are worm-like protozoans, and if eaten by certain small crabs, the life cycle is completed. Some inconclusive experimental evidence suggests that the gregarine spores cause mortality in oysters. However, since the spores do not undergo reproduction like spores of *Dermocystidium marinum*, they are not numerous, and they cause little pathological change in the oyster, the likelihood is greater for other factors being involved in the mortalities.

A bucephalid digenean (flatworm) also infects oysters in the northern Gulf of Mexico. Some infected individuals gape, suggesting harm caused by the fluke or an associated stress. Most infected oysters, however, become castrated, and their fullness and tastiness often improves like that of a gelded domestic animal. The improvement becomes noteworthy during the summer when the condition of uninfected oysters diminishes because of spawning activity. Even though eating oysters harboring the larval stages of this fluke may be esthetically displeasing, the consumer cannot be harmed. The larvae only infect specific fishes which in turn must be consumed by other fishes to mature. Man digests both larval and adult stages. Life cycles of other digenetic flukes, or trematodes as they are often called, will be discussed in detail later.

Any oyster in the Gulf can occasionally harbor a tapeworm larva, one or two larval roundworms, or a variety of amoeboid, ciliated, or flagellated protozoans. When the oyster undergoes stress, some of the protozoans reproduce extensively and become implicated in disease. Quantification of the role of those protozoans in oyster disease and mortality must await further investigation.

A few larger symbionts, visible to the naked eye, inhabit the oyster, but seldom harm it by themselves. Those most likely to arouse curiosity are a small snail, pea crabs, and turbellarian flatworms.

A 5 millimeter (mm) long (see glossary under measurements), whitish snail (commonly known as the impressed odostome) congregates in numbers sometimes greater than 100 at the edge of an oyster shell. Reaching over the edge, a snail intermittently protrudes its proboscis into

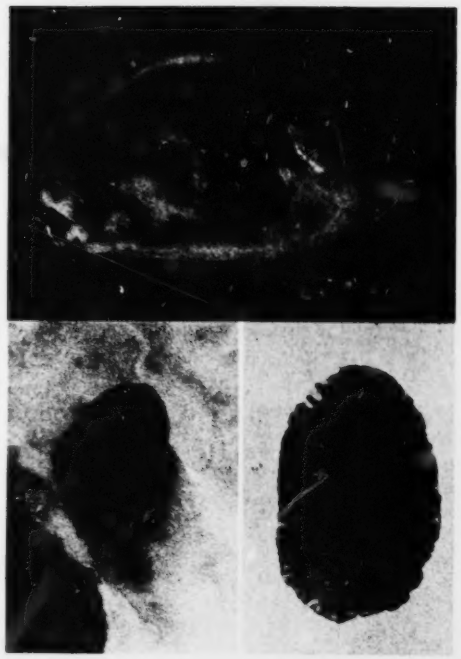
the oyster's mantle to feed on mucus and tissues. Not specific to the oyster, but apparently preferring it, the little gastropod also feeds on other molluscs and on polychaete worms. It is part of the high salinity oyster reef community*. Younger snails replace the older ones in late summer, more often inhabiting older oysters.

Pea crabs associate with a variety of invertebrates. One species, popularly referred to as the oyster crab, commonly invades oysters in New England and on occasion inhabits individuals along the northern Gulf, especially from high salinity reefs such as those off Pass Christian, Mississippi. Small crabs less than 1 mm wide enter an oyster, usually settling on the gill surface. Spat and year-old oysters appear to attract more crabs, even though the crab survives best in year-old and older oysters. The pinkish female crab grows along with the oyster until it reaches over 1 cm wide. In contrast, the male remains small and even has a hard stage which allows it to leave one oyster to mate with females in others. Usually one or two females occupy an oyster, but many can be tolerated.

Not feeding directly on the oyster, the crab nevertheless irritates and erodes the host's gills. To feed, it traps mucus and food masses in its walking legs, or it picks strings of food directly off the host's gills with its pinchers. Young crabs probably filter food from the water.

From a gourmet's standpoint, any diminishment caused in an oyster's condition is compensated for by the addition of a tasty morsel. In New England, pea crabs get eaten both raw and cooked. If cooked, the bite-sized morsels can be sautéed or deep-fat fried along with hermit crabs and small fish.

The oyster "leech," actually not a leech but a polyclad flatworm (Figures 9 to 11), lives among oysters and feeds on them or on associated animals such as barnacles. Occasionally, if an oyster cannot eject an entering worm by rapid closure, it will secrete a horny partition along the margin to keep the worm out. When oysters possess several such concentric partitions, oyster fishermen recognize that "leeches" have been present. According to some people, the flatworm has an easier time getting into spat than adults and periodically causes mortalities. Those infested adult oysters typically also harbor an infection of *Dermocystidium marinum*.



Figures 9-11. A polyclad flatworm (*Stylochus ellipticus*) commonly known as an "oyster leech." Top, the flatworm gliding across a 105 mm long oyster valve. Note the deeply-pigmented adductor muscle scar on the shell. The degree of pigmentation varies widely among individuals, and its presence differentiates the American oyster from the smaller Gulf oyster. The small dark areas surrounded by lighter areas result from the burrowing clam. Bottom left, close-up of same flatworm. Bottom right, a preserved and stained specimen of the same species. The worm feeds on oysters and barnacles, but seldom severely harms any oysters other than young or stressed ones.

Another related polyclad commonly occurs in the oyster drill, and it can even enter an oyster. If one wanted to collect any of the different polyclads, there is a trick to

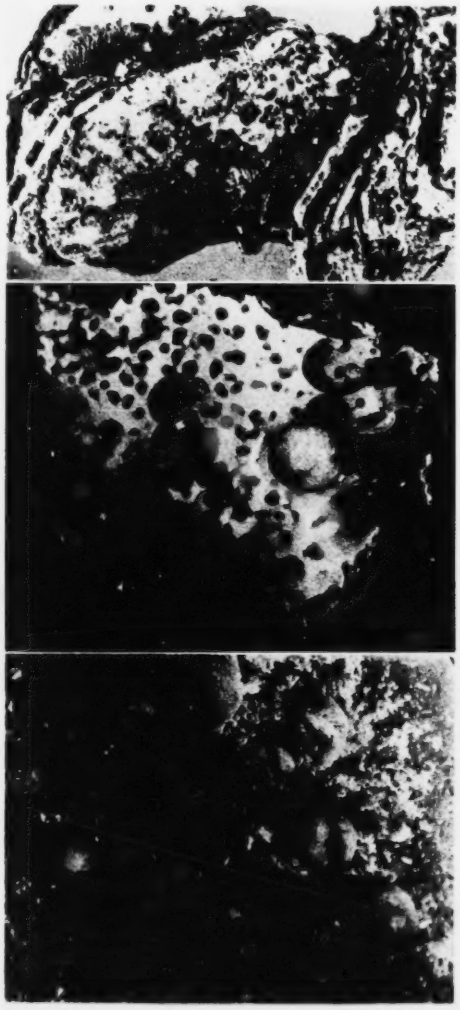
it. An easy way is to place oysters or crushed drills in a bucket of water from the mollusc's habitat and leave them for a day or so. Once the water fouls and loses its oxygen to decomposing hosts, the flatworms will crawl about on the side of the bucket and can be readily seen. Without a concerted collecting effort, many worms may be overlooked. Indeed, most fall off or dry up and are never seen by those who relish oysters-on-the-half-shell. An organic solvent such as xylene will cause these and many other hidden symbionts to leave their host, but use of such methods will kill the organisms.

With a dish of specimens plus some healthy hosts, some enterprising student should be able to design an experiment to study feeding and pathological effects on the hosts, to investigate survival or reproductive capabilities of the worms under different conditions, and to win a prize in a science fair. All species usually inhabit the mantle cavity of their hosts, but I have observed specimens inside a drill's shell near the top of the spire. What are they doing there? One species in a hermit crab's shell eats the crab's eggs, but, during other seasons, helps maintain the inner surface of the shell by feeding on fouling organisms.

Shell-Burrowing Symbionts

A few associations between oyster and symbiont involve species that burrow into the shell. Even though confusion exists concerning definitions, here I consider a burrowing animal one that excavates a space for the purpose of living all or a part of its life. In contrast, a borer is one which forms a hole in order to obtain food or inject a substance.

One burrower on high salinity reefs in Mississippi *(Diplothyra smithii)* commonly goes by the name burrowing (or boring) clam (Figures 12 to 14). The foot of a young individual secretes an etching or softening substance, allowing the serrated margin of the clam's shell to rasp and scrape a tunnel. The clam does not burrow indefinitely, only excavating as a juvenile. During summer months, spawning occurs and the larval stage with its developed foot finds and penetrates into an oyster or, less



Figures 12-14. The burrowing clam (*Diplothyra smithii*) in the oyster. Top, oysters show the diagnostic small round holes of the clam as well as the raised siphon-chimneys that protect the burrow from silt. Specimens of the hooked mussel occur on both margins of the middle oyster; the outer central portion of that oyster's valve became weakened and broke off because of clam burrows. Middle, valve has been purposefully broken to expose clam. The small irregular holes are sponge burrows. The conspicuous network of pits at the margin is actually an encrusting bryozoan. Bottom, adult burrowing clams removed from their final excavation site.

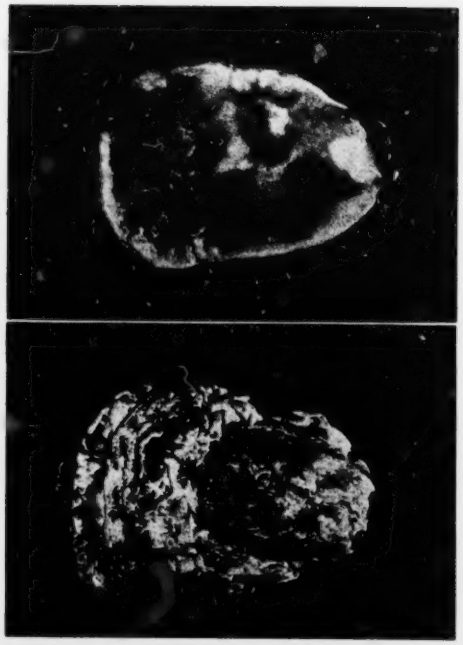
Figures 15-16. Radiographs of oyster valves. Left, the large opaque specimens of the burrowing clam are surrounded by the marginal U-shaped burrows of the mud worm. Right, the burrowing clam is surrounded by the network of cavities formed by a burrowing sponge. These photos are printed from negatives made by the same apparatus that X-rays teeth.

often, into the shells of a few other molluscs. After about 3 months of slow burrowing, the clam's incomplete shell begins to reach its full size and encloses the foot. That foot degenerates as the clam matures. At about 1 cm in length, the separate males and females remain stationary in the cavities.

Externally, this pest can be recognized by its characteristic small hole in the host's shell through which the clam receives food and oxygen and removes excreted waste products (Figure 12). Sometimes raised well above the shell, relatively high siphon-chimneys (note where oysters join in Figure 12) protect the clam from excess silt. When a burrow approaches or extends into the inner part of the shell, the oyster produces layers of a hard proteinaceous material (conchiolin) to reinforce the region. Nevertheless, burrows materially weaken the shell, making the oyster vulnerable to predation and less desirable to consumers because the shells crumble apart. As recently as 1975, Mississippi's oyster season was opened early for the lower reefs off Pass Christian because shells possessed numerous clams.

Two other culprits in Mississippi commonly burrow in shells, and these are depicted in radiographs (often called X-rays). Figure 15 shows both the clam and U-shaped burrows of mud worms, whereas Figure 16 reveals the numerous smaller excavations made by the burrowing sponge as well as the clams.

The mud worm, a polydorid polychaete *(Polydora websteri)*, forms mud blisters. Larval individuals, after developing first in egg capsules lining the adult's tube, become planktonic and then settle onto the outside of the shell or on the lip's margin to begin burrowing. What starts as small horseshoe-shaped depressions ultimately develop into large U-shaped encasements of mucus-cemented mud along the inner shell-surface covered by a host-secreted semitransparent material. Following stressful periods of high temperatures, often about November,



Figures 17 and 18. Oyster valve depicting the presence of the mud worm. Top, blisters resulting from the oyster's protective secretions. These signs also favor use of the name "blister worm." Bottom, reverse side of the same valve with typical external pits associated with the blisters.

mud worms commonly lack the oyster's thick, protective, nacreous covering. Figure 17 depicts diagnostic blisters, and Figure 18 of the other side of the shell shows the external pits associated with those same blisters. Whereas probably not killing an oyster, the presence of several of these annelids often signifies that the oyster is in poor condition.

Young (alpha-stage) burrowing sponges affect the shells of both living and dead oysters. In fact, they continue growing after the death of an oyster until large masses are formed. The size and shape of the small cavities (Figures 13 and 16) and the size and shape of the siliceous (glass) spicules, observable by dissolving away surrounding tissue with laundry bleach, characterize the several species of *Cliona*. Unless the oyster has grown very old or undergone excessive stress, it does not allow direct contact between its tissue and the sponge. It if does, black blotches may speckle the mantle, visceral mass, and shell. The extensive network of burrows creates rather brittle shells. Each species of yellowish-to-orange sponge seems to thrive best in different salinity conditions. Some species turn brownish when they die.

Fouling Organisms and Predators

A variety of animals grow on oysters. These fouling organisms do not parasitize them, but they may compete with them for food, smother them, or prohibit spat settling. Some of these are slipper shells, the hooked mussel, sponges, bryzoans, hydroids, tunicates, and barnacles. A polychaete *(Nereis [=Neanthes] succinea)*, much longer and greener than the reddish polydorid, commonly crawls among these fouling inhabitants and even feeds on gaping oysters, acquiring spores of *Dermocystidium marinum*. Occasionally one accidentally drops in with a shucked oyster to the disgust of a consumer.

Comments on predators should be made for a few reasons: one, to exemplify the difference between a parasite, which seldom harms a non-stressed host, and a predator, which eats and usually kills its "host"-prey; two, to relate that some predators, just like some disease-agents, can decimate large populations; and three, to emphasize that completion of some life cycles of parasites depends upon a predator.

A variety of oyster predators exists in the Gulf. The most devastating is the southern oyster drill, or conch, which will be treated in detail later. Another carnivorous gastropod, the lightning whelk, also consumes many oysters. It opens the oyster shells by chipping away at the valves until it can insert its proboscis. In some Atlantic coast regions starfish eat many oysters, but in Mississippi, blue crabs, mud crabs, and stone crabs rank as more important predators. A blue crab can consume many spat each day (Figure 19). It prefers 3 to 4 cm long individuals and seldom feeds on a large oyster unless it is damaged or unhealthy.

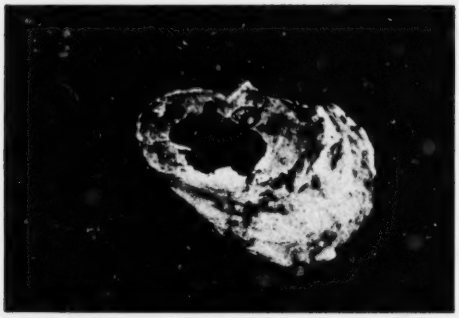


Figure 19. The valve of an oyster spat showing a hole made by a blue crab in order to eat the oyster.

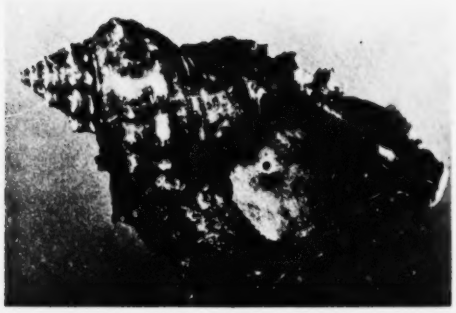


Figure 20. An oyster drill (conch) pulled back from a bored spat on an old oyster valve. All drills do not bore holes in their prey like the one shown here. When a drill does bore into its prey, the hole is often near the margin.

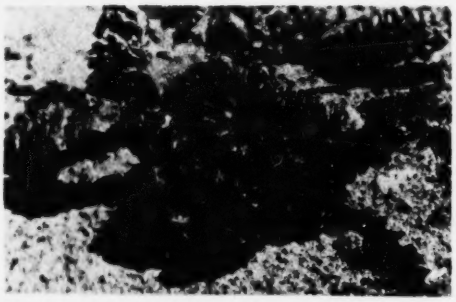


Figure 21. Snail (gastropod) egg-capsules on the beach. The lightning whelk produced the long string of capsules, the true tulip deposited the triangular ones attached to the string near the center, and the oyster drill attached the narrow ones visible above those of the tulip. If the embryos within the capsule of the drill die, a purple color stains it. A hole at the top indicates the young escaped.

Both mud and stone crabs help complete life cycles of parasites by feeding on oyster tissue. They are definitive hosts for gregarines and facilitate development and dispersion of *Democystidium marinum* spores. Other examples of life cycles will be presented in other sections. Fish such as the cow-nosed ray eat many oysters as does the black drum, which has well-developed pharyngeal teeth to crush the oyster's shell. Above all, man with his numerous devised means to collect and prepare oysters is the primary predator.

As indicated earlier, the southern oyster drill *(Thais haemastoma)* is generally the most devastating predator in the northern Gulf. It does not always bore into the shell of its prey (Figure 20). Aided by secretions, boring involves movement of the radula, a ribbonlike organ with rows of teeth, which rasps back and forth etching away shell material. Young moderately-sized drills usually bore oysters, especially large ones, near the edge of the shell, whereas older drills seldom bore at all. The drill apparently emits a paralytic agent, a yellowish secretion from the anal gland, that turns purple in sunlight. Oysters preyed on by drills often have purple stained tissue. A drill can devour a large oyster every few days and can kill nearly 100 week-old spat per day. Increased temperature usually increases feeding rates and weakens oysters which in turn can be disastrous to a reef.

Drills have a catastrophic effect because of their large populations. They undergo communal spawning, attaching egg cases to a hard substratum*. With up to 10 or more drills in a group, many young are produced. Each drill typically produces about 8, but sometimes up to 17, egg capsules an hour, and each of these encloses up to 900 embryos. A mass (Figure 21) often contains over 1000 of these 6 mm by 2 mm capsules. Following a storm, a beachcomber can observe masses of capsules washed up on the beach. The purple color discloses that the embryos died, whereas an open hole on the flattened top surface shows that the larvae escaped. The drill is dispersed over large areas because its larva is planktonic.

THE BLUE CRAB

As the most economically important crab from the Gulf and Atlantic states, the blue crab *(Callinectes sapidus)* is caught primarily in chicken wire "crab pots" and trawls by professional crabbers (Figure 22) and in drop nets or on a piece of twine by sports fishermen. Rather than being attracted to poultry parts, pork scraps, or fish using the above means, the soft-shelled stage of the crab does not feed and can be collected with a dip net or in an artificial shelter. This special gourmet's delight remains in the soft stage for several hours following molting. Molting will be described later, but of importance here to those who have never eaten soft-shelled crabs is that the entire crab minus gills, "apron*," and a narrow anterior portion provides a rich broiled, fried, or barbequed delicacy.

In most of the northern Gulf of Mexico, the adult crab may spawn once or twice during the 9 months from spring through fall as opposed to once in Chesapeake Bay where the crab concentrates spawning to about a 2 month period. Spawning occurs in high salinity regions, often near barrier islands in the Gulf. If not in high salinity water, the first larval stage (nauplius) held by the female and the next larval stage (zoea) die or do not develop properly. After developing in a highly saline habitat, the larva metamorphoses (into a megalops), migrates into estuaries, and metamorphoses again (to an early crab stage). Juveniles thrive in the estuaries; they commonly inhabit the soft muddy bottoms of navigational channels and marsh regions. They mature within a year, at which time a male typically fertilizes and protects the female during her final molt. Insemination occurs once in her life, even though the stored sperm may produce several "sponges" of eggs. Unlike the female, the male typically remains in the estuary and molts a few more times, in some cases for as long as 5 years. The advent of dropping temperatures, usually in conjunction with lowered salinities brought

Figure 22. Commercial crabber and his son emptying catch from crab pot into sorting tray.

on by winter northerly winds, usually signals females to leave the estuary. Atypical conditions like the extended high salinities in Lake Borgne, Louisiana, during late 1976 and early 1977 inhibited the migration, thereby causing a decline in the winter's crab catch in Mississippi Sound.

I presented the above features of the crab's life history because they dictate the kinds and amounts of symbionts that affect a crab. Molting represents an example. When a crab sheds its molt, it sheds many ectosymbionts. Discussion of some symbionts follows, not all of which are shed by molting.

Protozoans and Microbes

As true parasites, microsporidan protozoans infect a variety of host cells. Of at least five different species infecting the blue crab, one *(Ameson michaelis)* deserves special consideration because it harms the most crabs and its life cycle is the only one from the blue crab that has been established. Because it is an internal infection, it is not lost by molting, but it affects the crab's behavior.

"Sick crabs," the term used by some fishermen to designate individuals diseased with *Ameson michaelis*, occur commonly in a variety of habitats from Chesapeake Bay through Louisiana. Heavy infections can be recognized easily because muscle tissue acquires a chalky appearance in joints of

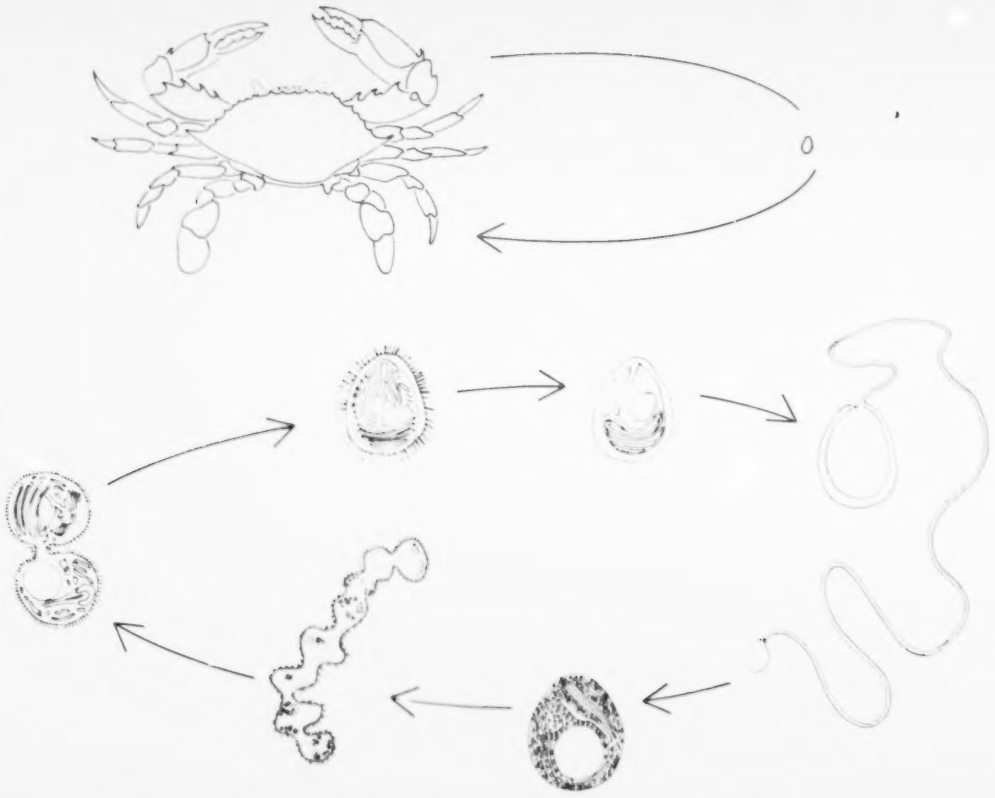


Figure 23. Life cycle of a microsporidan *(Ameson michaelis)* in the blue crab. The cycle of this protozoan is direct; there is no true intermediate host. When a blue crab feeds on infected crab meat or spores from another source, the long internal tubular filament of the spore turns inside out as it protrudes, allowing the infective nucleus and associated material to pass through it and infect a host blood cell. Divisions of the microsporidan within the blood cell produce a continuous supply of the parasite that reaches muscle tissue where there forms a string of developing spores. As a spore approaches maturity, there are first two joined cells and then a single mature spore. Crab meat infected with spores turns opaque and chalky. The muscle tissue surrounding the masses of spores breaks down, and the crab becomes weakened and vulnerable to stress.

the appendages and the abdomen often turns grayish. Even though virtually absent from Mississippi Sound until spring of 1978, sick crabs typically inhabit nearby Lake Pontchartrain and Lake Borgne in Louisiana. Generally less than 1% of the crabs there show infections, but occasionally more than this number linger in warm lagoons and close to shore. Perhaps this disease has a great impact on young crabs. In our studies, we have experimentally infected both young and old individuals without difficulty. Naturally-infected crabs as narrow as 2 cm across their carapace* have been seen, but small crabs avoid most routine collecting procedures by people who would recognize infections. Naturally infected crabs often fail to undergo migrations with noninfected counterparts, and they tend to die more readily when stressed.

Before learning about the life history of the infectious agent, fishermen would smash infected crabs and return them to the water, allowing noninfected blue crabs to feed on the tissue and acquire the disease. Education therefore helped the fishermen in a way similar to the situation when oyster fishermen from Chesapeake Bay and from Puget Sound, Washington, learned that for each starfish arm ripped off with a central portion, another predator starfish regenerated to feed on their crop.

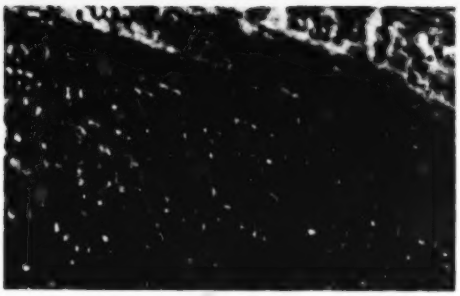


Figure 24. Highly magnified view of microsporidan spores (*Ameson michaelis*) among muscle fibers of blue crab.

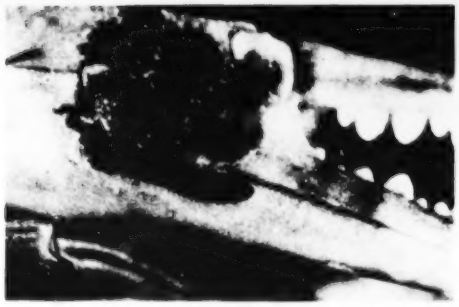


Figure 25. Claw of blue crab with shell-disease. This brownish lesion with degenerated internal regions apparently results from a bacterium (*Benekia* type I) which digests the chitin from the exoskeleton. An infection is rarely fatal and is lost during molting of the host.

A diagram (Figure 23) reveals an extremely magnified representation of stages in the cycle. A mature spore (Figure 24) measures about one-fourth that of a human red blood cell (1.9 microns [μ] versus 7.6 μ). Under appropriate conditions, an ingested spore everts its long internal tube (polar filament), an action roughly analogous to blowing out the inverted finger of a rubber glove. The nucleus and cytoplasm of this single celled animal squeezes through the extruded pliable filament and invades a host crab's blood cell. Once there, the organism undergoes vegetative growth, producing cells which in turn produce strings of eight individual spores along muscle tissue. Ultimately, enormous numbers of these resistant spores and their products destroy adjacent tissue and replace the crab's normal musculature. This parasite can be considered highly host-specific* because the muscle tissue of only *Callinectes sapidus* exhibits infections. Many symbionts, like the bacteria mentioned in the next paragraph, have a wide, or loose, host-specificity* because they associate with a wide range of hosts.

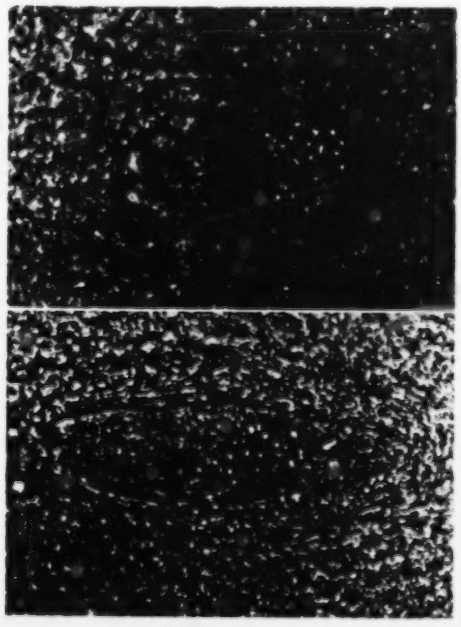
Shell disease ("box burnt" crabs) represents a typically non-fatal microbial condition usually initiated by a wound. In any event, infected crabs usually have not molted for a long period and have undergone stress. Starting as brownish areas with reddish brown depressed centers forming on the exoskelton, these lesions develop into deep necrotic* pits (Figure 25) that typically do not penetrate through the shell. Once the thin external lipid (fat) layer of the shell (epicuticle) has been disrupted, the exposed chitin* becomes digested by specific bacteria and possibly also fungi. Probably fewer crabs than lobsters die from the disease, especially if lobsters are cultured in warm water. Death probably results from secondary infections. Nevertheless, crabs look esthetically displeasing, and confinement fosters disease. Hence, some crabbers know the disease as "box burnt" because they maintain crabs in floating cypress-box cages waiting for their catch to molt.

Certain other bacteria harm both crabs and people, when given the proper conditions. One such organism (*Vibrio parahaemolyticus*) readily kills crabs and causes food poisoning in people. In crabs, species including *Vibrio parahaemolyticus* cause large jelly-like blood clots in addition to whitish-colored nodules to develop in the gills and elsewhere from masses of aggregated blood cells and bacteria. Crabs from Mississippi waters occasionally die from these infections. In people, numerous cases of intestinal upset associated with eating seafood probably also result from this organism. Even minimal heating, however, eliminates this threat. To avoid food poisoning in crab-preparing operations, continued care should be taken not to permit fluid from fresh crabs to contaminate previously-

boiled crabs. Additonal difficult-to-diagnose microbial diseases of crabs will appear following the section on metazoans and their hyperparasites•. Metazoa, not a natural group of organisms, designates that an included organism is multicellular with two or more tissue layers.

Metazoans and their Hyperparasites

Larval flukes (digeneans), unlike larval tapeworms (cestodes) (Figures 26 and 27), infect many freshwater, estuarine, and marine crabs. Microphallids form a family of digeneans that utilize three hosts: 1) a snail as a first intermediate host•, 2) a crustacean as a second intermediate host, and 3) a bird, mammal, or rarely a cold blooded vertebrate as a definitive host. At least six species infect the blue crab. We will mention two, the first (*Levinseniella capitanea*) because it can be seen easily among the gonads or the diverticula of the digestive gland if the crab's carapace• is removed. Nearly 4 mm long, the excysted worm ranks as the largest microphallid known. Most other species average less than 1 mm, appearing somewhat similar to a comma in this booklet in both size and shape. Also very unusual, *Levinseniella capitanea* has no gut or muscular pharynx, principal features for most larval microphallids and used by almost all adult digeneans for feeding. The gut does not develop even after the larva in its spherical, yellowish cyst has been eaten by and matures in a raccoon.



Figures 26 and 27. Two views of same larval tapeworm moving through muscle of lesser blue crab (*Callinectes similis*). Although apparently common in this crab, it has not been observed in the common blue crab (*Callinectes sapidus*).

The second species (*Microphallus basodactylophallus*) can barely be seen in crabmeat (striated muscle tissue) without a microscope, unless a urosporidan protozoan has hyperparasitized it. It measures about 0.45 mm (450 microns) long after removal from the spherical 0.35 mm cyst (about the size of the following period).

Figure 28 illustrates the life history of this digenean. Any of four species of snails from the shallow low salinity estuaries• may release the infective free swimming larva (cercaria). That free-living larva was produced in quantity within another asexual stage (sporocyst) which was itself produced by a similar larva that in turn had developed from a germ ball within the initial ciliated larva (miracidium). The initial larva occupied the egg which was fed on by the snail. In other words, from one egg develops an enormous number of larvae infective to the blue crab and at least two of the several species of fiddler crabs. Also, each resulting adult worm produces an enormous number of eggs. Because of dependency on environmental parameters and on need for specific hosts, these large numbers of eggs and larvae are necessary to assure completion of the cycle for one or more individuals and continued survival of the species.

Each individual possesses both male and female organs, making it hermaphroditic. It can successfully fertilize itself, even though all tested species of digeneans prefer to utilize partners, if given the opportunity. These worms mature when an appropriate final host eats the infected crab,

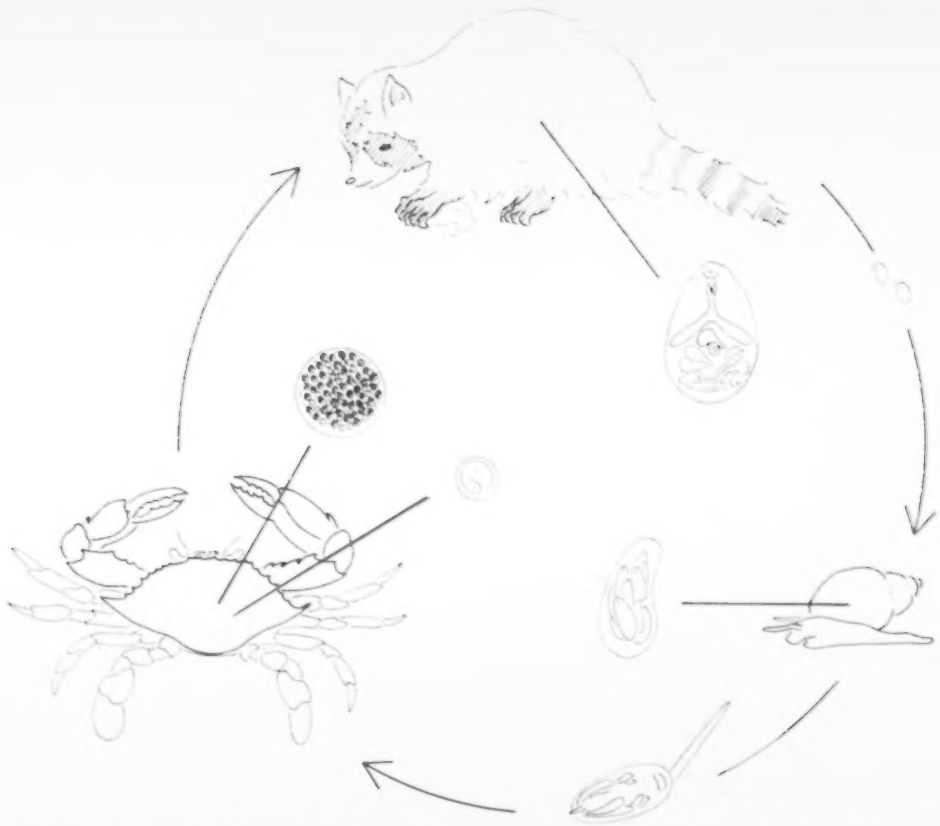


Figure 28. Life cycle of the microphallid fluke *(Microphallus basodactylophallus)*. The blue crab harbors the infective larva, sometimes hyperparasitized by a haplosporidan protozoan *(Urosporidium crescens)* which allows the infected fluke to impart the names "buckshot" or "pepper spot" to involved crabs. When eaten by an appropriate host such as a raccoon, the healthy larva develops into an adult and produces eggs infective to a few different estuarine snails. Asexual reproduction of the fluke occurs in a snail, as it generally does for all digeneans, and ultimately results in a tailed, swimming larva that penetrates the crab, loses its tail, encysts, and develops into a stage infective for the vertebrate.

assuming the larva has developed for at least a month in the crab. In Mississippi, the raccoon and marsh rice rat serve this need, but some birds and other mammals also fulfill the role. If a person ate a heavily-infected raw crab, he would probably acquire an infection and possibly develop minor gastric distress. Even though an infected person's health probably would not be seriously affected, a related species has been known to cause extensive gastric and neurological disorders. I recommend cooking crabs!

Local coastal residents have never disclosed to me any concern about eating crabs, presumably because they did not see any internal parasites. I assume they did not see the flukes because when such digenean cysts have a protozoan hyperparasite*, people often exhibit apprehension.

The minute, brownish, hyperparasitic haplosporidan *(Urosporidium crescens)* infects tissues of the encysted worm. This protozoan undergoes extensive multiplication until the cyst increases in size by many times and the worm's tissue has been replaced by spores (Figure 28). The vast number of spores in a cyst distinguishes each cyst as a visible black speck. Some fishermen term these cysts "buckshot" or infected crabs as "pepper crabs." Although severely debilitating the worm, the spores

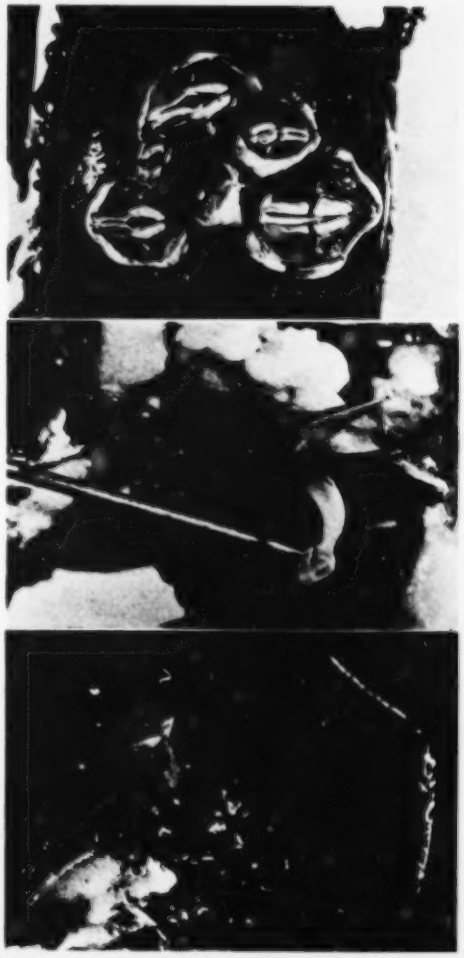
Figure 29. Buckshot, or pepper spot, in blue crab meat. Dark, almost spherical objects near the pointer and at the top of the meat are fluke larvae (*Microphallus basodactylophallus*) infected with a protozoan (*Urosporidium crescens*). The immense number of spores enlarges the fluke cyst many times. The piece of crab has been cooked; the exoskeleton for the swimming leg occurs in the lower left of the photo.

harm neither the crab nor man. A piece of cooked crab (Figure 29) reveals a couple of clusters of buckshot. Other encysted digenean larvae also harbor this or related species. Some also possess other kinds of protozoan hyperparasites including microsporidans, myxosporidans, flagellates, and opalinids.

The blue crab, a crustacean, has its own crustacean symbionts. Those discussed here, however, appear much different from the crab except for the early larval stage. They are barnacles and range between being fouling organisms and true parasites.

One common barnacle *(Balanus venustus niveus)* found on a variety of hard substrata• in the Gulf also establishes itself on the carapace and legs of the blue crab. Another, the acorn barnacle *(Chelonibia patula)*, exhibits more host-specificity•. It restricts itself to the external surfaces of a small group of crabs. Figure 30 shows it on the blue crab. Whether lacking or expressing specificity towards the crab, both encrusted barnacles cause their host hardship by producing excess weight which sometimes constitutes a considerable burden.

A gooseneck, or pedunculate, barnacle *(Octolasmis muelleri)* confines its presence to the gill region of a few decapod species,



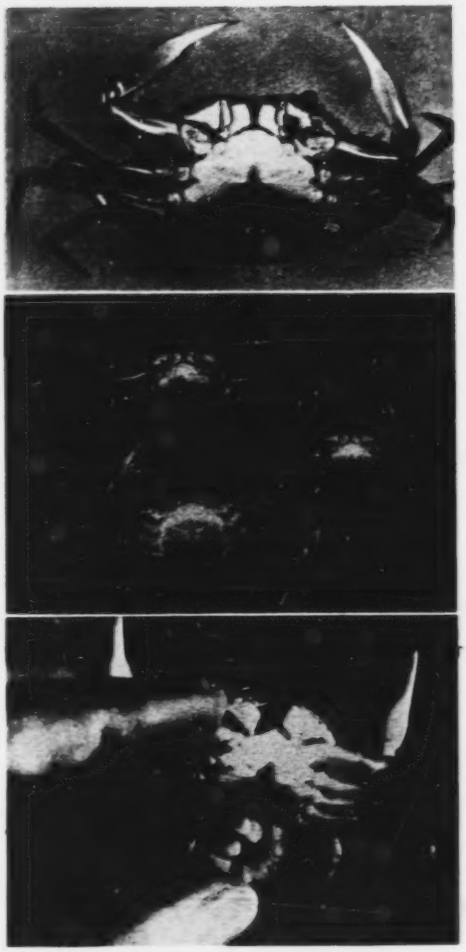
Figures 30-32. External barnacle symbionts on the blue crab. Top, the acorn barnacle *(Chelonibia patula)* on the carapace. Middle, a goose-neck barnacle (*Octolasmis muelleri*) on a gill filament propped up by a dissecting pin. Bottom, underside of gills showing many medium-sized and small *Octolasmis muelleri*. Note how few can be seen without lifting the gills.

including the blue crab (Figure 31). It needs a living crab for survival. Special cleaning appendages sweep gill surfaces free of debris and presumably of settling organisms. Once an individual does become established, the crab's cleaners apparently become less efficient. Consequently, increasing amounts of debris and numbers of larvae can settle on the gills. In fact, a crab can acquire over 1000 such barnacles on the gills and elsewhere in the gill chamber. When

small-and medium-sized barnacles infest a host, over 700 can coat the underside of the gills without hardly being apparent on the top surface of the gills (Figure 32).

The combination of these heavy infestations• and debris can make respiration difficult for the crab because barnacles compete for oxygen and decrease the amount of gill surface available for respiration. Healthy crabs are hardy; they live for long periods out of the water when their gills are moist, but die quickly immersed in stale water. Infested crabs act sluggish most of the time and probably attract predators.

The last barnacle to be discussed truly parasitizes its host (Figures 33 to 35). If not for being able to recognize its larval stages, biologists would not have been able to classify it as a barnacle. An external portion of this rhizocephalan *(Loxothylacus texanus)* protrudes from under the crab's abdomen (Figure 33). This bulge, called the externa, contains a brood pouch for larvae and both male and female gonads. A crab can have as many as eight externae, and three are fairly common (Figure 35). The remainder of the barnacle consists of root-like structures penetrating through most host tissues (interna). Crabs become infected when young by a swimming larva (cypris). After a period of internal development, the interna of the organism penetrates through a crab's soft abdominal joint when the crab molts. Infection retards a host's growth, leaving most externae-bearing individuals between 3 and 8 cm wide. Additionally, secondary sexual characteristics of infected males transform into those of females. Therefore, most infected crabs appear as miniature adult females, either with or without externae. The size-difference between an egg-bearing (sponge or berry) female and an infected crab is usually great. Figure 34 shows the size-difference between an uninfected immature female with her acutely pointed abdominal apron and a smaller infected crab with the transformed rounded apron normal for mature females. Castration of the crab may result from involvement with a structure called an androgenic gland. Male crabs have this



Figures 33-35. Sacculinid barnacle (*Loxothylacus texanus*) of the blue crab. Top, the protruding pouch (externa) under the crab's abdomen contains larvae and gonads (ovary and testes). Long, narrow extensions invade most other tissue. Middle, top crab has dark externa indicating an older infection than that of the yellowish externa of the middle crab. The larger lower crab reveals the small size of infected crabs. It is an immature female, wheras the aprons on the infected crabs reveal the apron of a mature crab. Infections also modify the shape of the male's abdomen into that of a female. Bottom, crab with three developing externae. Usually only one externa occurs per crab, but occasionally over five may be present.

gland, and, if it is removed from a young individual, female characteristics, including ovarian tissue in the testes, develop. Perhaps destruction of this gland or some action on its secretions, possibly additionally involving hormones produced by the barnacle's ovary, causes feminization of the infected crab.

Crabs with externae can molt and lose that part of the parasite, but whether that process is typical is unknown. Most biologists assume crabs with this and other mature rhizocephalans do not molt.

Infections, although prevalent in some high salinity bays and bayous in Louisiana, have been negligible until 1977 in Mississippi Sound since an epizootic outbreak in 1965. While aboard a shrimp boat in July 1977, I noted over half the crabs we trawled in the Sound exhibited infections. The apparent magnitude of infection in the population could be exaggerated because the small crabs would be continually thrown back by shrimpers for others to recapture, whereas large ones would be saved for eating. Nevertheless, infections occurred commonly for several weeks, and epizootics will undoubtedly occur again.

As with other cited barnacles, infections relate directly with salinity and probably with temperature. In inshore regions with moderately high salinity water, crabs have a greater potential for infection. Infections usually coincide with breeding and maturation peaks of the blue crab, being most prevalent about May and October in Louisiana.

Unlike the other barnacles attached to the crab, the adult rhizocephalan cannot tolerate low salinity. Maturing externae apparently do not protrude, and ones already protruding take on water and rupture. Low salinity habitats characteristic of Mississippi estuaries certainly do not favor barnacle infections.

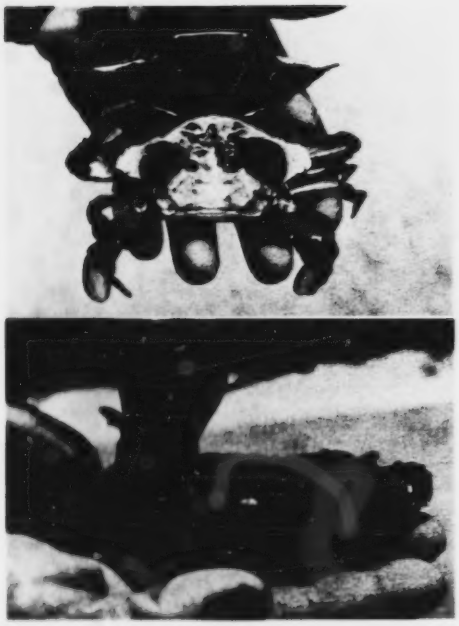
The presence of "dwarf" or "button" crabs concerns some fishermen. Do these small apparently sexually mature individuals that show up mostly during spring

Figure 36. Sacculinid barnacle parasite (*Loxothylacus panopaei*) in the mud crab (*Eurypanopeus depressus*) from Chincoteague Bay, Virginia. Note difference between this species and the one in the blue crab.

and early summer in Mississippi result from a distinctive genetic stock, from environmental influence, or from a parasitic infection? It seems quite possible that these crabs possess prepatent* sacculinid infections, and, indeed, that problem needs attention.

Mud crabs, much smaller crabs than the blue crab, also possess a related rhizocephalan barnacle, and the externa of that species (*Loxothylacus panopaei*) differs (Figure 36).

An understanding of molting aids interpretation of barnacle-crab associations and other symbiotic relationships for crustaceans. Like most crustaceans, the blue crab has a hard external skeleton also known as a cuticle* or shell. In order to increase in size, the crab must shed the old shell. When initiating this molting process (ecdysis), a new soft shell forms beneath the hard one of this "peeler" stage. Enzymes begin to dissolve the shell, allowing the products to be resorbed into the body-proper. Thus, amino acids, calcium, and other products can be salvaged for incorporation in the new cuticle. The posterior part of the old shell then cracks, allowing the "buster" stage crab to wiggle out backwards. This amazing process is controlled by a balance of separately-produced molt-inhibiting and molt-



Figures 37 and 38. Blue crab molting. Top, molt, or ecdysis, including covering of gills and lining of fore- and hindgut. Crabs that back out of shells like this remain extremely soft and pliable for about 4 or 5 hours. Bottom, soft-shelled crab. Note pliable nature of the twisted claw and depressed carapace.

stimulating hormones. The results are the discarded molt (Figure 37) and the helpless soft-shelled crab enlarged by 20 to 60% of its previous size (Figure 38). The crab imbibes and otherwise incorporates water while still soft in order to achieve the expanded size. After about 5 hours, unless retarded or halted in a refrigerator, the new shell hardens because the protein becomes tanned and calcium chloride is redeposited. Even though not as soft, this "paper-shell," or "buckram" crab will remain vulnerable to predators for another day or so.

As mentioned earlier, following mating, a female rarely molts again. Consequently, the shell of a mature female offers a prime substratum• on which barnacles and other fouling and symbiotic organisms can attach. In addition to being able to shed some symbionts by molting, the mature male usually inhabits low salinity habitats not conducive for barnacles.

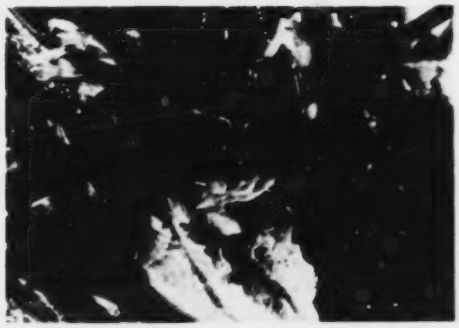


Figure 39. Long orange ribbonworm (*Carcinonemertes carcinophila*) pulled out from between gill lamellae. Other light colored regions on gills are additional specimens. The orange color indicates that the worm fed on the crab-host's eggs; thus, the crab had spawned. Also, note the barnacles on the gills. Both the ribbonworm and the barnacle indicate that the crab had inhabited high salinity water.

A ribbonworm (nemertean) *(Carcinonemertes carcinophila)* approximately 1.5 cm in length often inhabits the space between gill lamellae in crabs from high salinity water (Figure 39). Since, in the northern Gulf, most males do not accompany females migrating to salty regions in order to spawn, fewer male than female crabs have nemertean infestations• (see infection in glossary). This higher prevalence for females also acts in the best interest of the nemertean because in order for the worm to achieve sexual maturity and reproduce, it must migrate from the gills to the egg mass of the host. While there, it builds a mucus tube for inhabitation. Crab eggs provide nourishment for the worm, transforming the worm's color from creamy to orange. Because of the large quantity of yolk material, crab eggs appear orange during the first 5 days of the larva's 14-day developmental period. Since a crab can produce over 2 million eggs and may generate those twice in a year, even a heavy infestation by the nemertean has little effect on crab production.

Some time after mating, the female worm leaves her collapsed tube with its attached eggs. The resulting ciliated larva hatches and stays in the tube, swims among the crab

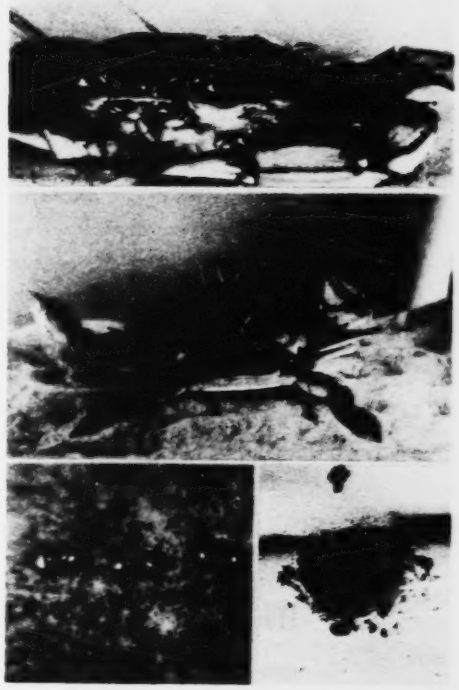
eggs, or leaves the host and undergoes metamorphosis into a creeping stage that infests another crab. The blue crab is the common host, but other portunids (swimming crabs) and occasionally nonrelated crabs harbor the worm. Because of an attraction by both the nemertean larva and the crab toward light, the two often come into contact and infestation occurs readily.

As indicated above, worms change color after feeding on crab eggs. Consequently, since adults return to the host's gills, the presence of orange worms encased between lamellae reveals that such a host crab has spawned at least once. The worm is a biological indicator! Strangely though, these tags lose some of their adult characteristics and may not feed at all during the winter.

A leech *(Myzobdella lugubris)*, unlike the nemertean and barnacles, conspicuously inhabits crabs in low salinity regions (Figures 40 and 41). Even though a case of numerous leeches associated with a few dying crabs implicates them in harming the crab, I doubt the leech causes lesions in the crab. The leech often occurs on considerable numbers of crabs in Mississippi and adjacent areas, but I have seen no evidence suggesting a harmful relationship.

After seeing Humphrey Bogart covered with leeches in the *African Queen* and hearing tales of people having their blood sucked while walking through tropical rain forests or wading through swamps, people have a tendency to be disgusted by the intriguing jawless leeches that thrive in our local fresh-to-marine habitats. Perhaps the thought of losing blood intensifies when people realize that in 1863, doctors used 7 million medicinal leeches *(Hirudo medicinalis)* on their patients in London hospitals and almost that same number in Paris. The practice of bloodletting in Europe declined soon after, but occasionally someone will still pull one of these from a culturing jar to remove blood from a bruise and alleviate swelling.

Even though many leeches do not suck



Figures 40-43. Leech (*Myzobdella lugubris*) on blue crab. Top, several specimens of the leech on the crab's anterior. Middle, several specimens on crab's posterior; most individuals deposit cocoons near the rear margin. Bottom left, cocoons on carapace. Bottom right, enlarged cocoon. A single young leech emerges from each cocoon; it develops in low salinity water and searches for a fish in order to obtain a blood meal.

blood, the crab leech does. Soon after hatching, it obtains its first blood meal from a fish. In Mississippi, a specimen of the southern flounder, striped mullet, or Gulf killifish may have several individuals attached to its gills, opercles, nostrils, fins, or body surface. Other estuarine fish may also possess this or other species of leeches, but usually in lesser numbers. The white catfish acts as a good host in regions where it enters brackish habitats. After receiving an adequate amount of blood, the engorged leech transforms from a skinny reddish worm about 1 cm long to a robust greenish-brown worm which can stretch a distance

greater than 4 cm.

The engorged crab leech typically associates with vegetation and throughout its life shows some ability to swim. Since the blue crab also associates with vegetation, the two come in contact. The leech then deposits adhesive cocoons near the rear margin of the crab's carapace (Figures 42 and 43). Often many leeches infest one crab. Based on observations of leeches attaching cocoons to finger bowls, some individuals probably attach their cocoons on other hard surfaces, also. In addition to providing a substratum• for cocoons, the crab offers a means of dispersing the leeches.

A single young leech develops within each cocoon. It can swim after emerging, and, like its parent, prefers water with little or no salt; neither stage tolerates much more salt than 15 ppt. The young leech must infest a fish to continue its cycle.

A leechlike organism also infests the blue crab in low salinity and freshwater habitats of Alabama, Mississippi, and Louisiana. This branchiobdellid *(Cambrincola mesochoreus)* shows phylogenetic• affinities to both leeches and oligochaetes (the latter being best known for earthworms and aquatic worms used to feed tropical fishes). About 2 to 3 mm long, this pink colored worm infests both the gill chamber and the external shell-surfaces without causing its host apparent harm. It feeds on small protozoans, algae, and detritus, and its presence suggests that the host crab has been in fresh or nearly fresh water for some time.

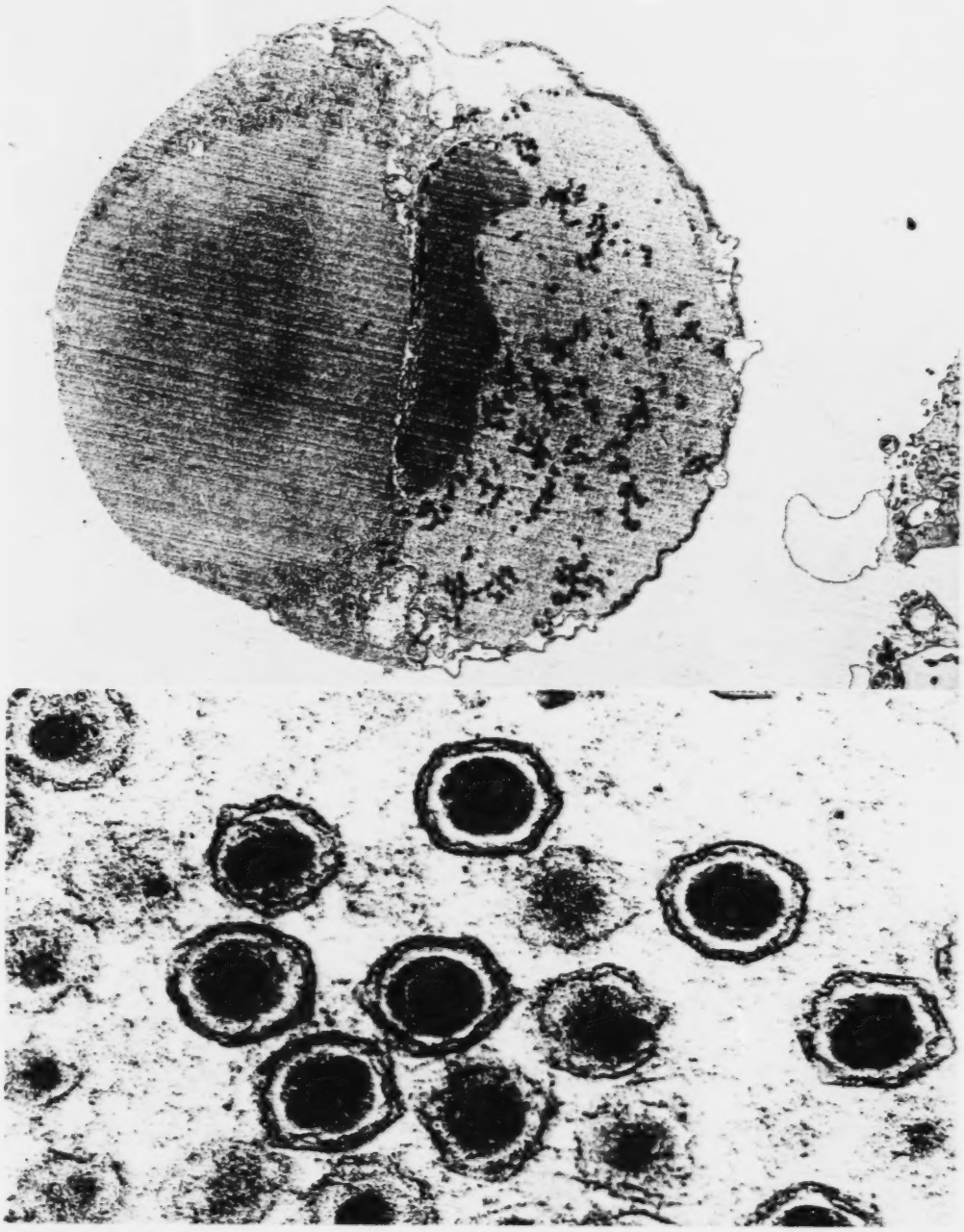
Miscellaneous Microbes and Protozoans

The crab harbors many more organisms than those already discussed. Most necessitate a microscope to observe individually, but a few can be seen when present in large numbers or when the crab shows signs indicative of specific infections. An electron microscope is needed to confirm the presence of some organisms. I will briefly comment on some of these microscopically-sized organisms, none of which has been implicated in human disease.

At least four different viruses infect the crab. Figures 44 and 45 provide an ultrastructural view of one of these. Until recently, few viruses had been reported from any invertebrate. Of the four in the crab, three cause fatalities when the hosts are kept captive. They occur in crabs along the eastern U.S. coast, and, if examined for in the Gulf, some would probably be found. Little has been learned about any of them or their relationships with the crab host.

A severely pathogenic amoeba *(Paramoeba pernicosa)* causes mortalities in the blue crab from high salinity habitats along the eastern U.S. coast. It is treated here because of the potential for it to be introduced or to be present already, but unrecognized, in the Gulf. The causative amoeba occurs in connective tissues and blood (hemal) spaces throughout the infected crab's body during all times of the year, but enters the blood and kills the host primarily during summer. When amoebae enter the blood, the ventral portion of the crab, especially a male, becomes grayish in color, and, if the disease advances to this state, the crab always dies. Crabs with this "gray crab disease" may have all their blood cells destroyed and replaced by the amoeba. The nonclotting hemolymph• acquires the grayish tint from the organisms. By this stage of the disease, the host's stored nutrients have been depleted, making recovery unlikely. Some crabs of all sizes, sexes, and stages, however, can overcome light infections and survive. Hemocytes• engulf or encapsulate the protozoan, and other individuals are destroyed by humoral• mechanisms.

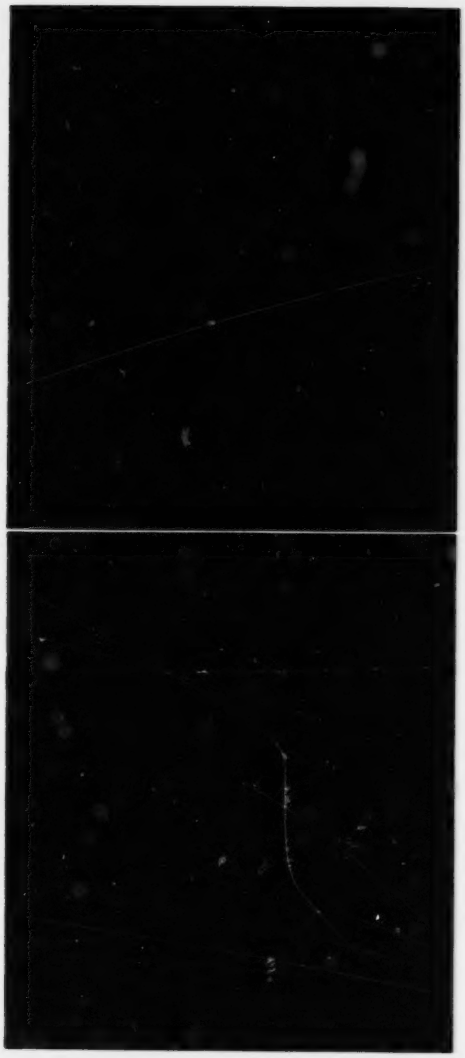
The presence of even low grade amoebic infections has not been discovered in the Gulf. If that absence results from geographical barriers and not from insufficient examinations or from some biological or environmental reasons, it becomes imperative not to introduce eastern crabs into the Gulf. Crabs are already transported in the opposite direction. Seafood companies routinely ship live Gulf crabs to the



Figures 44 and 45. Electron micrographs of herpeslike virus from blue crab. Top, note dark-staining virus particles in crab's blood cell. Bottom, close-up of virus particles. (Photos magnified 4,550 and 67,000 times, respectively).

east coast where they attract great profit as a food item.

A few ciliate protozoans infest the crab. One *(Lagenophrys callinectes)* produces its own "house" or lorica• (Figures 46 and 47). Within this small, about 55 micron diameter (about nine would touch end to end across the narrowest width of the letter i) transparent dome, the common animal inhabits lamellae of the gills of crabs from both the



Figures 46 and 47. Different preparations of a loricate ciliate (*Lagenophrys callinectes*) from the gills of the blue crab. Note the aperture in the transparent lorica.

Atlantic and Gulf coasts. It can control the lips at the opening near one margin, and it feeds on nonhost matter. Another loricate ciliate, an undescribed suctorian (*Acineta* sp.*, see sp. in glossary) occurs among individuals of *Lagenophrys callinectes* in Mississippi. In contrast, a stalked ciliate (*Epistylis* sp.) usually attaches to the margins and stems of the gill lamellae rather than the flat portion. None of these ciliates seem to harm the crab. Most hosts are old, and perhaps the ability of heavily-infested crabs to respire becomes diminished under stressful situations.

Internally, a "holotrich" ciliate moves about with the hemolymph. Even though present in large numbers in some dying confined crabs, this protozoan also occurs in healthy crabs from Mississippi. Presumably, the potential for these and other protozoans to become hazardous to crab health increases considerably when crabs are reared or kept captive in water of poor quality.

Crabs from North Carolina to the Gulf harbor a parasitic dinoflagellate (*Hematodinium* sp.) in the hemolymph. The organism, about the size of a crab blood cell, infected 30% of a sample of crabs in Florida. It causes tissues to appear milky and the blood to clot (like with infections of gram negative bacteria); the dinoflagellate may be responsible for numerous mortalities, especially those occurring during autumn in habitats with salinity greater than 11 ppt.

A haplosporidan (*Minchinia*-like) related to the organism in the oyster has been encountered in moribund crabs from Virginia and North Carolina. It causes hemolymph to become milky and not clot. No spores have been observed.

Critical examination will uncover additional protozoans on or in the gills, appendages, hemolymph, and muscles of the blue crab. Some of these have never been reported.

Large numbers of dead crabs occasionally line some of the high salinity beaches in Mississippi and Louisiana. I have never seen these crabs, and biologists have assumed that the old crabs, mostly spawned-out females heavily infested with barnacles on their gills and shells, died of old age. Perhaps some of these also had complicating protozoan or viral infections!

In addition to infesting crabs, disease organisms also involve crab eggs in the Gulf and elsewhere. I already discussed a nemertean larva feeding on eggs. A fungus

(Lagenidium callinectes) invades them. In salinities of 5 to 30 ppt, up to 25% of an egg mass may be infected. Infected eggs are smaller and more opaque than healthy ones. The diseased portion of the sponge, which is always at the periphery, appears brownish rather than yellowish-orange or grayish when the crab's larvae have developed enough to give the healthy part of the sponge a brown or blackish appearance. Infections become a real concern for people rearing crustaceans, especially since larvae can become infected. On the other hand, infections can aid natural populations; the fungus also infects the ova of the symbiotic barnacle *(Chelonibia patula)*.

PENAEID SHRIMPS

The valuable shrimp fishery in the northern Gulf of Mexico includes primarily three species: the brown shrimp *(Penaeus aztecus)*, the white shrimp *(Penaeus setiferus)*, and the pink shrimp *(Penaeus duorarum)*, the latter being much more important in southern Florida than in the northern Gulf.

All species spawn in high salinity regions; their larvae develop in the offshore plankton• before metamorphosing into postlarvae and invading the estuarine• nursery regions. Of all the shrimp, the pink shrimp requires the highest salinity water; it also prefers a sandy-shell habitat. Brown and white shrimp thrive in muddy-sand or silty habitats, where, in about 30 to 50 meters of water, the brown shrimp can be caught in large numbers during night hours between June and August. It remains commercially abundant down to 110 meters. On the other hand, the white shrimp moves about during the day and occurs more commonly in water less than 18 meters deep with salinity less than full strength seawater. Consequently, the white shrimp is available for small inshore trawlers, usually between August and November.

Postlarval shrimps invade the estuary at different periods, with most brown shrimp arriving about March and most white shrimp during the summer. As both become juveniles, the white shrimp can be found further up bayous and rivers than brown shrimp; the white shrimp remains longer in inshore regions.

The number of these young shrimp that will enter the commercial fishery depends not on the number of spawning adults, but on the temperature, amount of freshwater, and other environmental conditions that affect survival and growth. These factors also have a bearing on the parasites and diseases of shrimp hosts.

Adults usually live 1 to 2 years, spawning two or more times. Some individuals, however, survive a few additional years and these shrimp usually possess quite an assortment of symbionts. Shrimp of all ages and stages harbor parasites, and the parasites occur in many sites. Figure 48 of a brown shrimp indicates many of these sites occurring in all species.

The majority of parasites and disease conditions affecting shrimp, unlike those affecting most marine organisms, have been investigated in some detail. Still, a weekend fisherman or even a commercial shrimper seldom recognizes many of the conditions. In fact, those people rearing shrimp and encountering heavy mortalities rarely know the causes. Although blamed for many shrimp-kills, low oxygen concentration levels may not always be the sole culprit. The shrimp may have to harbor a symbiont in addition to being exposed to low oxygen levels in order to succumb.

Because shrimp diseases are well documented, I will discuss several of the conspicuous ones as well as some parasites that could be encountered from a high percentage of shrimp if a curious individual decided to dissect his specimens and use a microscope.

Microbial Diseases

Unlike most viral diseases known from crustaceans, one *(Baculovirus penaei)* involves the digestive gland of shrimp, and

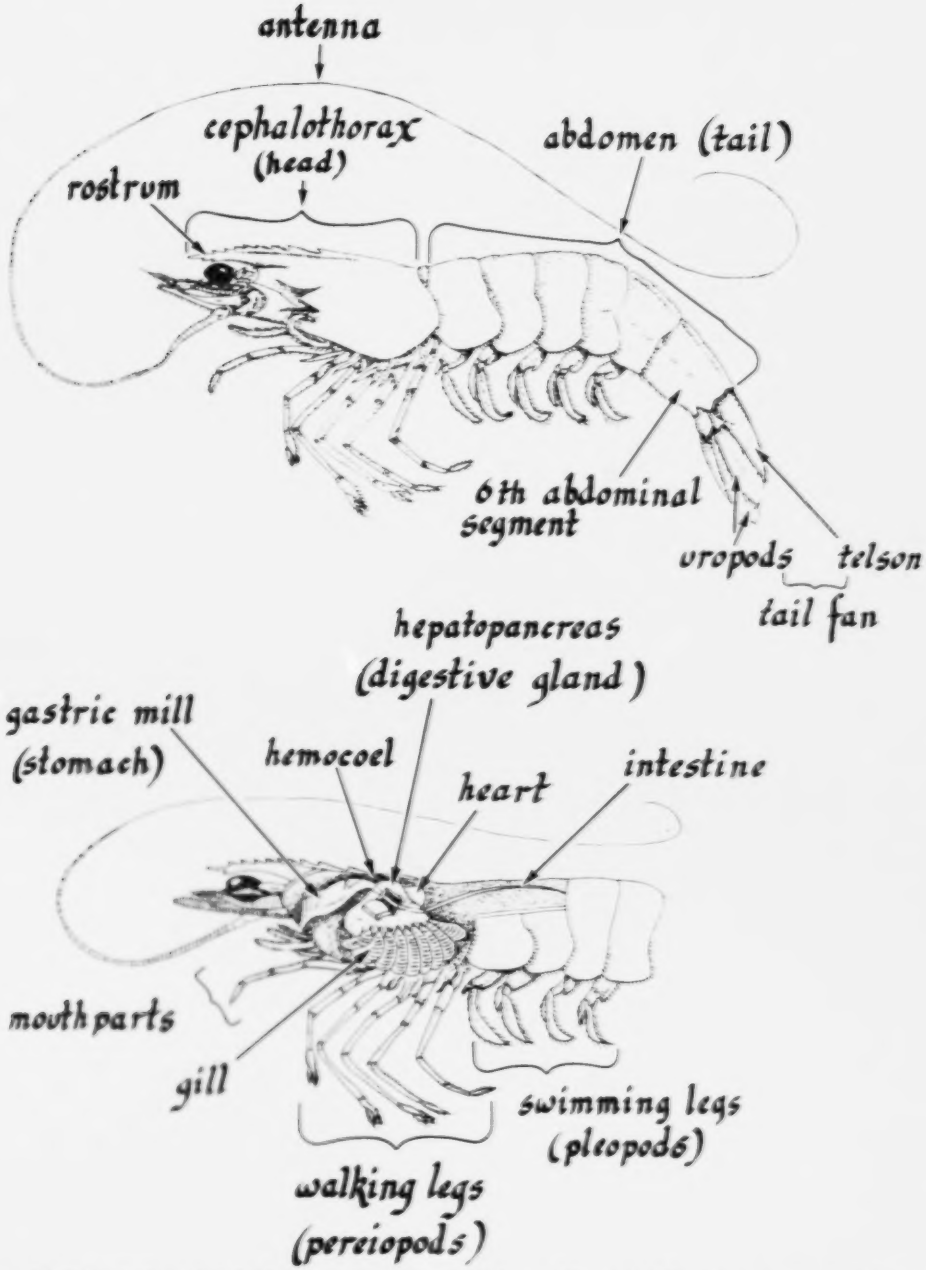
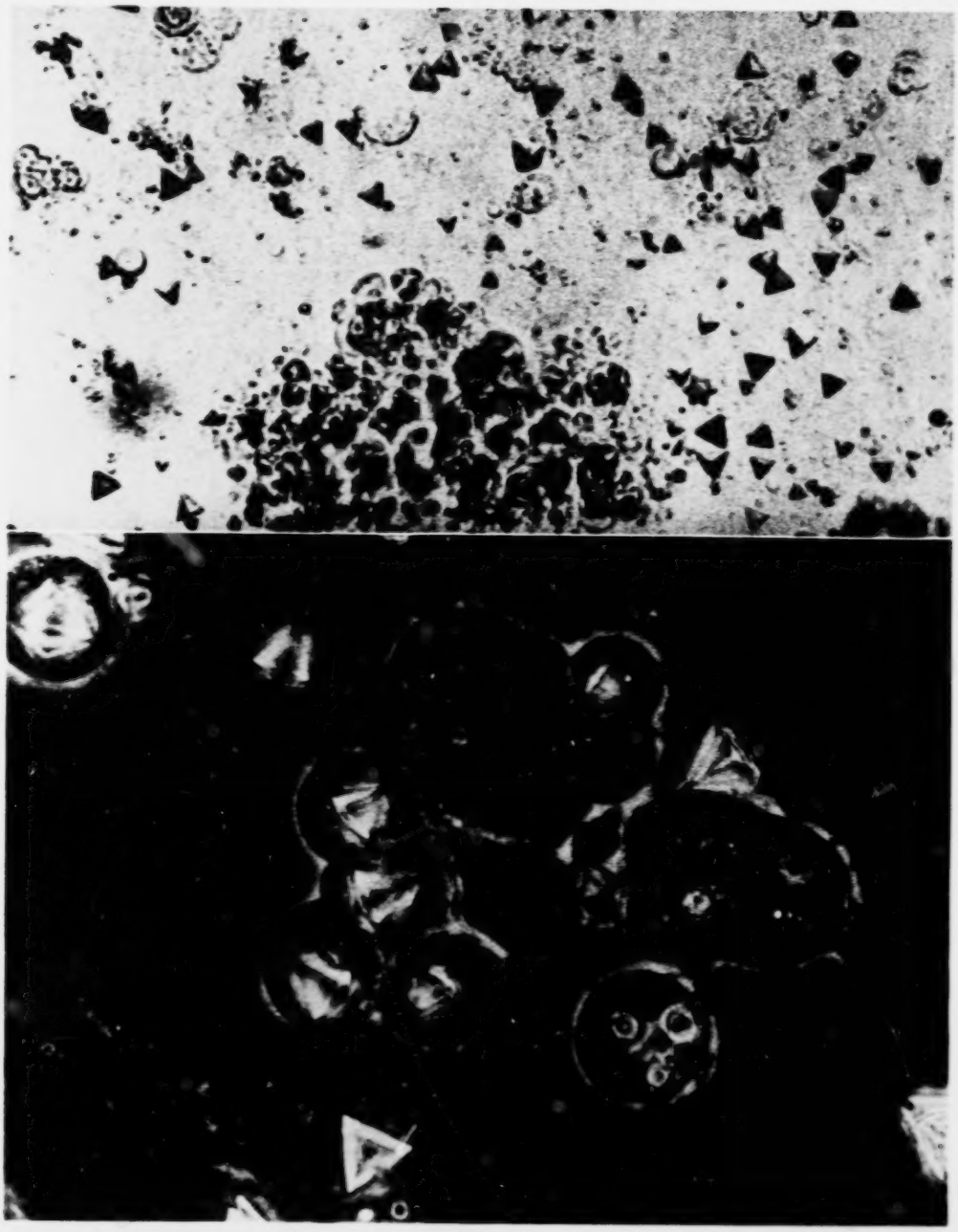


Figure 48. Selected anatomical features of brown shrimp with part of the carapace cut away from the lower specimen to show internal structures.

indications of its presence can be seen with a regular microscope. These signs include a relatively large refractile polyhedral-shaped inclusion body* and swollen nuclei and other cellular alterations of the hepatopancreas (Figures 49 and 50). Inclusion bodies do not have to be present in infected shrimp. Perhaps these obvious bodies act as a means to protect and disperse the virons when the host is eaten or otherwise dies.

Shrimp, either crowded in a tank or exposed to polluting polychlorinated



Figures 49 and 50. Inclusion bodies for virus *(Baculovirus penael)* in digestive gland of shrimp. Top, note most inclusion bodies are tetrahedrons. They encase virus particles. Bottom, a phase-contrast close-up showing the refractive inclusion bodies within the nucleus of the digestive gland cells as well as others that are free.

biphenyls or Mirex have a tendency to exhibit an increased number of inclusion bodies. Such individuals also tend to die more readily than shrimp without these bodies. For mortalities to be caused by the virus in nature, some pollutant or antagonist may have to be present. The virus affects pink, brown, and white shrimps at least in

Figures 51 and 52. Brown shrimp with shell-disease. Bottom, disease-condition occurring in site of wound. Lesions in both shrimp possessed a bacterium (*Beneckea* type I) which digests chitin in the exoskeleton and probably caused the disease.

Florida and Mississippi and probably infects many penaeids wherever they occur.

Chitinoclastic organisms including bacteria cause shell disease, or black spot disease, in shrimps (Figures 51 and 52) as well as in the blue crab and other crustaceans. The lesion in Figure 52 illustrates a wound inflicted by a predator. Such infections are usually lost with a molt, and rarely does an affected shrimp die from this alone. When specific bacteria (*e.g.*, a chitinoclastic variety of *Vibrio anguillarum*) involve pond-reared shrimps, death can occur. Indeed, low grade mortalities, apparently not resulting from secondary infections, have plagued reared-shrimp production in Mexico.

Shrimps, just as the blue crab, host a variety of internal bacteria, some of which cause extensive mortalities in pond-reared hosts and others that do not affect the host. The white opaque gill filaments of a white shrimp from Mississippi Sound shown in Figure 53 probably exemplify a bacterial

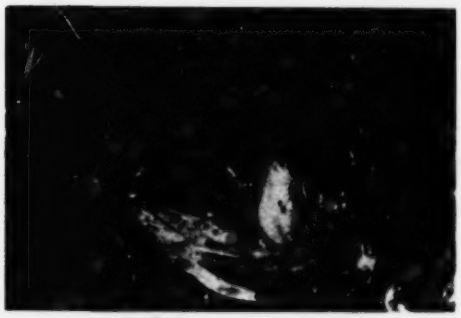


Figure 53. A white shrimp with some white-colored gills probably caused by a bacterial infection. Many host blood cells crowded together in the affected gills.

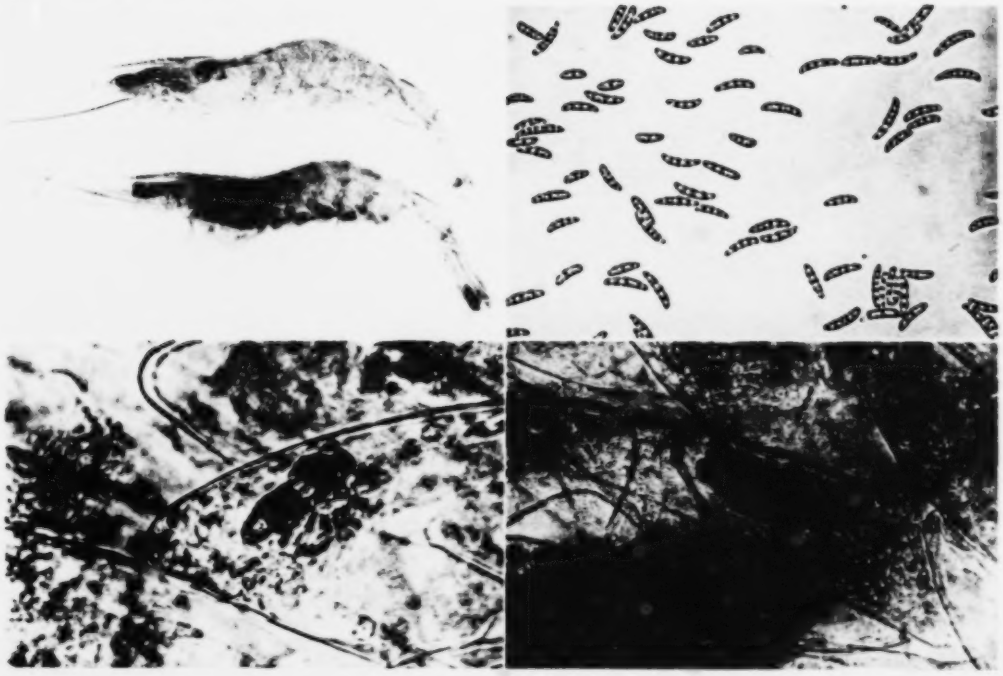
infection. A massive hemocytic response involved the area, producing the opaque condition.

Black gills or "black gill disease" can result from a bacterial infection, but more often this multicaused disease results from other agents, and a few of these will be discussed later.

Externally, a filamentous bacterium (probably *Leucothrix mucor*) entangles larval shrimp, and it, along with considerable trapped debris, probably inhibits respiration and otherwise burdens the host. As with most diseases, reared shrimp usually constitute the primary victims. The same or a similar bacterium also occurs on a variety of crustaceans, fishes, and plants.

Shrimp, as well as a variety of other marine animals, can harbor *Mycobacterium marinum*. This bacterium, related to the tuberculosis agent of man, can cause a skin rash (dermatitis) on those susceptible people who handle shrimp or other seafood products. Reactions differ among people: some have hard pustules on their hands whereas others have blisters.

A variety of fungi infects shrimps, but most have not been cultured or investigated. One that has been investigated (*Fusarium solani*) shows variation in its virulence to different penaeid shrimps. A response by the host hemocytes to spores and hyphae* in the gills can result in a deposition of dark pigment (melanin) producing "black gill disease."



Figures 54-57. Fungal black gill disease. Top left, brown shrimp with disease compared with uninfected individual. Top right, spores *(macroconidia)* of causative agent *(Fusarium solani)*. Bottom left, host response by shrimp blood cells after 24 hours. Bottom right, increased pigmentation (melanization) apparent by 28 hours. The text discusses several other agents that cause black gill disease.

Deposition of brown-to blackish melanin pigment occurs in shrimp that have been wounded, have been exposed to foreign materials, and have fungal (see Figures 54 to 57), protozoan, or helminth infections. In some cases, the tissue underlying the carapace• and not the actual gills is darkened. Perhaps waste products (nitrates or ammonia) discharged through the gills or even precipitation of materials (metallic sulfides) produces the condition.

Protozoan Infections

What's a cotton shrimp? Four species of microsporidan protozoans infect commercial shrimps in the northern Gulf. Three of those infect and replace nearly all the abdominal muscle tissue of their hosts, resulting in an extremely opaque condition somewhat similar in appearance to a cooked shrimp (Figure 58). Shrimpers refer to these hosts as "cotton shrimp" or "milky shrimp." The name "cotton shrimp" also reflects the texture of the cooked product.

Figure 58. Tails of the brown shrimp; the top shrimp exhibits cotton shrimp disease. Three different species of microsporidans cause this milky or chalky appearance of tails of penaeids in the northern Gulf of Mexico. In this case, tiny spores of *Ameson nelsoni* surround and eventually replace the muscle bundles.

The fourth microsporidan species (*Agmasoma penaei*; Figure 59) is more

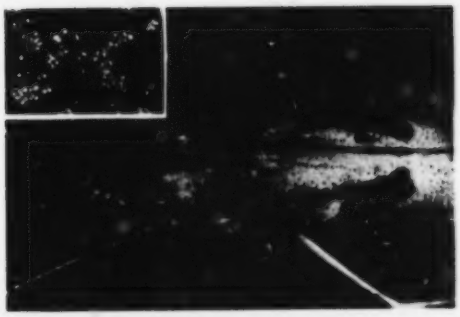


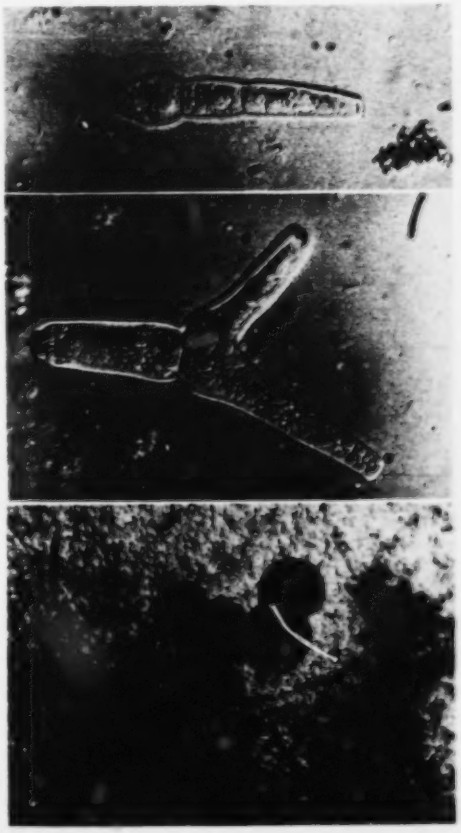
Figure 59. Chalky appearance under cuticle reflects microsporidan (*Agmasoma penaei*) that invaded blood vessels under the carapace of the white shrimp. Usually, tissue along the middle portion of the top of the tail exhibits infections by this protozoan. An insert shows some spores in the typical packet of eight. Others have broken loose from the membrane, and one spore (macrospore) is typically much larger than the others.

host-specific than the others and does not infect the tail. Involving primarily the white shrimp, an infection appears most distinctly along the dorsal midline of the tail and under the carapace in the cephalothorax. Many people think that infected gonads and intestinal tissue are ripe ova ready to be released. Consequently, some prefer the taste of these "ripe" shrimp over noninfected shrimp.

More than one species of microsporidan can infect an individual shrimp. In fact, three species in a single shrimp can be visually differentiated by their color and location if the tail is cut crossways.

Infected shrimp react poorly to stress conditions. Usually, when compared with their noninfected counterparts, they die more readily when handled, are more vulnerable to predators, and do not normally partake in migrations. Often many shrimp caught inshore exhibit microsporidan infections. In these cases the bulk of the shrimp stock may have previously departed to other waters; however, a few cotton shrimp do occur in offshore catches, suggesting that some infected individuals migrate and survive.

Several protozoans other than microsporidans have symbiotic relationships with penaeids. Also, all species of shrimp in the northern Gulf harbor a cephaline gregarine (*Nematopsis penaeus* or some other indistinguishable species). The motile stage (trophozoite) can be seen attached to or gliding about in the intestine, sometimes with as many as seven individuals joined end to end in a chain or branched so as to exhibit a forked posterior end (Figures 60 and 61). Two attached individuals develop into a spherical cyst that embeds in the shrimp rectum (Figure 62); the cyst in turn produces a stage infective for some yet unknown mollusc.



Figures 60-62. A cephaline gregarine from the white shrimp. Top, an association of three individuals in a chain gliding about in the intestine. Middle, a forked association. Bottom, cysts (gamontocysts) embedded in rectum. These result from encystment of associations and can barely be seen as a chalky-colored dot with unaided naked eyes. Stages in the rectum infect appropriate molluscan hosts.

For another similar appearing species (*Nematopsis duorari*) restricted to pink shrimp, the shrimp acquires infections by feeding on mucus trails of several common bivalves including the Atlantic bay scallop, broad ribbed cardita, cross-barred venus, and sunray venus.

These and at least two more gregarine species that attach to feeding appendages probably cause no more than minor disease in either the shrimp or the corresponding molluscan hosts.

Ciliated protozoans occur in as much variety as do gregarines. On the gills, colonies of a stalked peritrich (*Zoothamnium* sp.) give a brownish cast to the gills when enough of these organisms attach. The attachment of the stalk to a gill examined with an electron microscope reveals no pathological alterations. The simple attachment of a small colony can be seen in Figure 63. However, when a large number of the ciliate infests the gills, as it can when hosts are crowded or placed under specific environmental conditions, shrimp often die. Death usually coincides with periods of low concentration of the water's oxygen, a common condition following several warm overcast days or following decomposition of a large algal bloom. The ciliate apparently competes for the available oxygen because shrimp with few colonies of the organisms often survive the stress whereas those with many die.

Figure 63. A colonial ciliate (*Zoothamnium* sp.) on the gills of a commercial shrimp. The dark fiber extending along the stalk's center permits the entire colony to contract simultaneously. Note the cilia at the top of the bell which direct food particles into the organism. The protozoan harms shrimp only when certain environmental stresses arise.

A related species (*Epistylis* sp.) differs from *Zoothamnium* sp. primarily by lacking a central contractile fibril within the stalk. Thus, it cannot contract its stalk. The fibrils (myonemes) of *Zoothamnium* sp. connect where the stalks branch, allowing simultaneous contraction or expansion of an entire colony and a wonderful show when seen under the microscope!

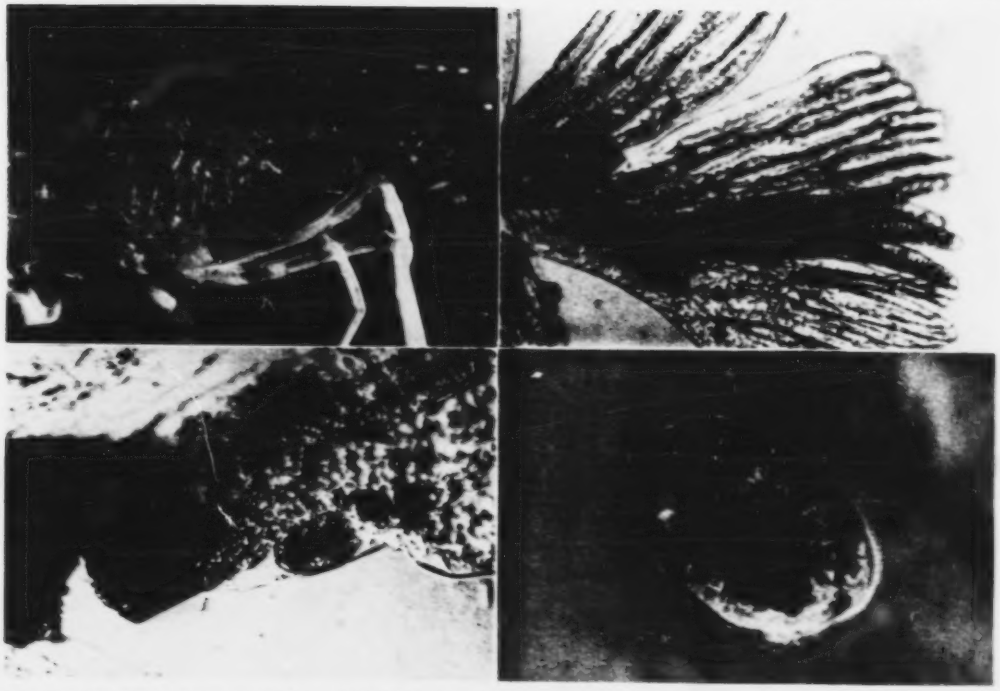
Unlike *Zoothamnium* sp., *Epistylis* sp. usually infests the appendages and exoskeleton-proper rather than the gills. Both species infest larval shrimp and present treatable threats to cultured shrimp. The effect on natural populations has not been established.

Another unnamed ciliate encysts on or in gills. Common where distal gill filaments branch, this nonstalked apostome also causes black gills (Figures 64 to 67). Specks of melanin surround the ciliate. The life cycle of this foettingeriid has not been established, and several technical papers confuse it or a similar species with loricate forms like the one on the blue crab. External loricae*, however, have apertures surrounded by lip-like structures and thereby provide an easy means of differentiation.

Other protozoans can be seen by carefully examining shrimps from a variety of habitats. Relationships among some of these with the host remain obscure. An unidentified suctorian species of *Ephelota* on the exoskeleton looks entirely different from the one on crab gills. An internal ciliate (*Parauronema* sp.) which can fill the entire hemocoel and a flagellate (*?Leptomonas* sp.) which also occurs internally have been implicated in larval mortalities, possibly in conjunction with the virus *Baculovirus penaei*.

Helminths

Shrimps act as second intermediate hosts for a few digeneans. For those species with spherical cysts enclosing the larval worms, infections are localized primarily in the tail.



Figures 64-67. A brown shrimp with "black gills" caused by an apostome ciliate. Top left, part of carapace removed to show dark specks on gills. Top right, close-up showing apostomes and melanin pigmentation. Bottom left, close-up showing individual ciliate under the cuticle with the associated melanin. Bottom right, close-up of ciliated stage.

whereas the elongated cyst of one species occupies the cephalothorax.

The spherical cysts all harbor microphallids which develop to maturity primarily in mammals and birds. Figure 68 shows an experimentally infected white shrimp with one of the several species that infect it. Most shrimp microphallids infect their hosts in inshore low salinity regions and probably follow a life cycle similar for that shown for a species in the blue crab (Figure 28).

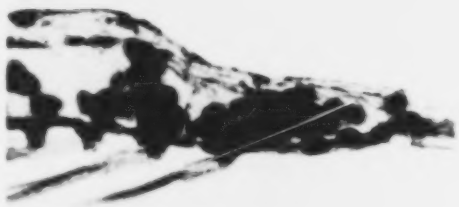


Figure 68. A penaeid shrimp experimentally infected with a microphallid fluke larva (metacercaria).

On the other hand, the species with larger elongated thin cysts found in the hemocoel adjacent to the alimentary tract typically infects shrimps from high salinity water in Mississippi. The worm *(Opecoeloides fimbriatus)*, about 2 mm long when excysted, has a pedunculated ventral sucker with small papillae on the surrounding lobes. The same frilled appearance of the sucker exists for the mature worm in the gut of a fish (usually a drum or croaker of the family Sciaenidae) that eats the infected shrimp.

Larval tapeworms (cestodes) occur in two principal sites: in the digestive gland and in the intestine. Almost all cestode species in shrimp from the northern Gulf utilize elasmobranchs as final hosts: one encysted one may use a bird, and a small single suckered mobile species in the intestine has not yet been correlated to its adult form. An individual shrimp often harbors more than 1000

Figure 69. Larval (plerocercoid) tapeworm from intestine of commercial shrimp. Over 1000 individuals of this small unidentified larva can attach by their single sucker to the gut of a single shrimp.

specimens of this larval intestinal cestode (Figure 69), and large numbers may harm the shrimp.

Because most prevalent, most studied, and most conspicuous in all penaeids from the Gulf, one larval trypanorhynch, or tetrarhynch as it is also called *(Prochristianella hispida)*, will be treated in detail.

Crustacean-feeding stingrays *(Dasyatis sabina* and *Dasyatis sayi)* harbor mature *Prochristianella hispida* in their spiral valve (an adaptation of the intestine to increase its surface area). Figure 70 diagrams the life cycle. Segments (proglottids) with partially developed eggs break free from the tapeworm and pass out with a ray's feces.Once in seawater the proglottids split open, liberating many eggs, each with two thin, sticky

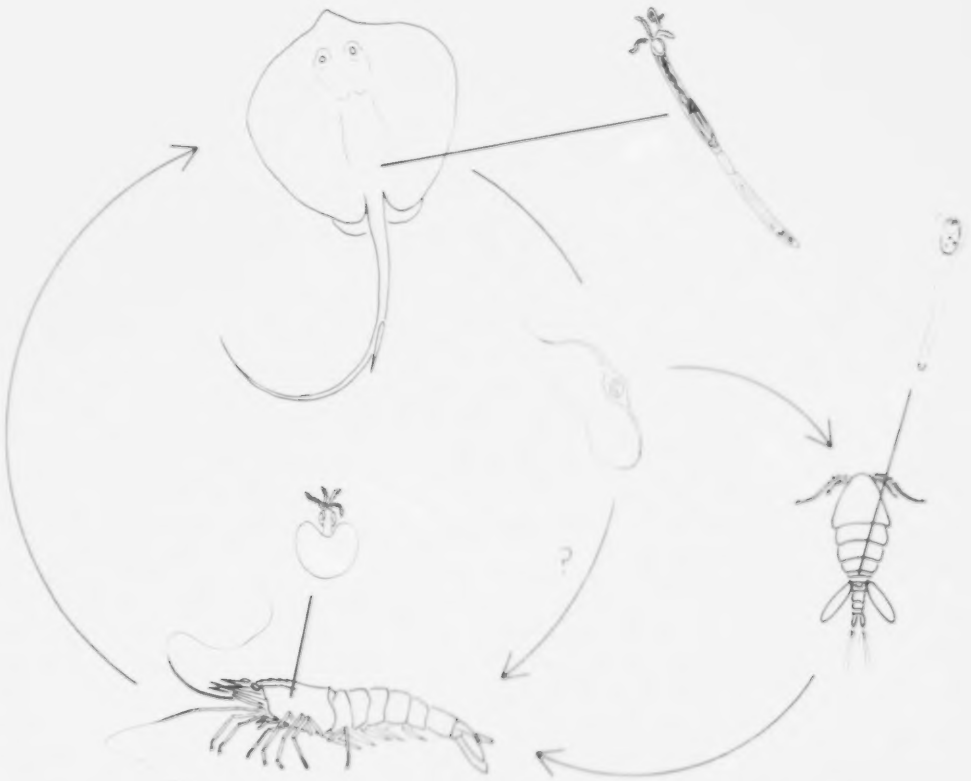


Figure 70. Life cycle of a trypanorhynch tapeworm *(Prochristianella hispida)* in commercial shrimps. Stingrays harbor the adult worm in their spiral valve. Terminal segments drop off the worm and release eggs that develop larvae when in seawater. The enclosed larva develops in copepods. Whether shrimp obtain their infections from eggs or from copepods has not been established, but rays probably acquire infections from various shrimps.

Figures 71 and 72. Larval stages of a trypanorhynch cestode (*Prochristianella hispida*). Top, filamented eggs with larvae clumped together. Bottom, blastocysts, each with enclosed larva (plerocercoid) in the digestive gland of a penaeid shrimp. A portion of the pigmented membrane covering the digestive gland has been removed on one half to expose digestive caeca. Three whitish cysts are apparent on the pigmented membrane.

filaments (Figure 71). A single hooked larva (oncosphere with six anchor-like hooks) within the egg develops to an infective stage in about 4 days. Whether shrimp get infected by eating food with entangled eggs or by eating infected copepods has not been established. A larval form (procercoid to plerocercoid) develops in the hemocoel of some copepods and may progress similarly in a variety of shrimp, or possibly a shrimp may have to eat the infected copepod. A hard capsular cyst surrounds the early plerocercoid within the fleshy procercoid-like stage (blastocyst) when in the copepod. This encystment has never been seen nor reported from shrimp and might be a transitory developmental structure present only under certain conditions. On the other hand, other crustaceans such as the ghost shrimp, which possesses blastocysts larger than those in penaeid shrimps, may be the ray's most utilized crustacean host. In order for the cycle to be complete, the ray eats an infected crustacean. The blastocyst, but not the actual plerocercoid, can be seen in a shrimp without disturbing it if the cyst protrudes through the host's membrane covering the digestive gland (Figure 72). Some individual blastocysts occur entirely within the gland and elsewhere within the hemocoel.

The adult trypanorhynch attaches to the ray's gut by means of four eversible hooked tentacles. A tentacle turns itself inside out. By the size, shape, and arrangement of the hooks, one characterizes the several species that infect penaeids as well as other species that parasitize a wide variety of crustaceans, molluscs, fishes, and occasionally other hosts. These attachment structures remain unchanged from the late larval to adult stage.

Larval roundworms (nematodes) also infect penaeids and several other hosts. Most common in a variety of fishes and invertebrates including shrimp is an ascaridoid (*Thynnascaris* type MA). Several individuals of this worm and a smaller number of a smaller member in the same genus (*Thynnascaris* type MB) occur commonly either coiled and encysted or free in the digestive gland, among other tissues of the cepahlothorax, or occasionally in the tail portion of the shrimp. The smaller species (type MB) may be a health hazard. Within an hour after being eaten by a mouse, it can penetrate into or through the wall of the mouse's alimentary tract and cause a host-response. Some individuals live for a considerable time in the mammal, whereas the host reacts against and quickly kills others. In any event, the potential exists for a person to develop a severe inflammatory response after eating raw seafood harboring the worm or to express a hypersensitivity reaction from worms eaten subsequent to the initial infection. Such conditions, with symptoms similar to those for an ulcer, appendicitis, or cancer, have affected people in Japan, the Netherlands,

and other places where people consume raw seafood harboring related nematodes. Either cooking or subzero freezing prevents human infections!

Life histories and identifications of the larval nematodes have not been established. Just as with the trypanorhynch, I do not know if shrimp acquire infections by eating larvae directly, by eating copepods with infective larvae, or by other means. The final host must be a fish and several species of these nematodes exist in the Gulf of Mexico and elsewhere.

One reason why so many individual hosts may harbor the same species of larva is that an individual worm may penetrate through the alimentary tract of a predator after being eaten along with a previous host and reencyst in the mesentery or elsewhere, remaining infective for another predator that in turn eats and retains it. Not until acquired by a proper definitive host will the worm molt and develop to maturity. Parasitologists call these hosts in which no development of a worm occurs "paratenic" hosts. These hosts allow completion of a cycle in cases where the definitive host rarely feeds on the true intermediate host. The worm may increase in size, but it does not develop additional features. A similar pattern of life cycle probably occurs for most related ascaridoid nematodes and these will be diagrammed and discussed more later.

Even though quite rare in penaeid shrimp, another larval nematode *(Spirocamallanus cricotus)* completes its cycle in a wide variety of fishes. Whether shrimps actually constitute a necessary link in the cycle has not been established, but they probably do not because other invertebrates also host the larva of this dramatic worm. It will be figured and discussed in more detail in the section on fish nematodes because it is in fish where the large reddish adult worm is most easily visible and most commonly found.

Even though other larval nematodes infect penaeids from other parts of the world, the only other fairly common nematode that I have seen in Gulf shrimp is what appears to be a free-living* nematode (*Leptolaimus* sp.). *Leptolaimus* sp. in shrimps from Louisiana to Alabama appear able to live in and on shrimp without being digested. The tolerance by the shrimp and relationship between worm and shrimp require further investigation; all related nematode species thrive without hosts in muddy-sandy habitats, and this one probably also lives in such a habitat. Many strictly free-living nematodes exist in water and soil, and notably few of these possess any strong family ties to any of the symbiotic species from aquatic hosts.

Miscellaneous Diseases and Attached Organisms

One amazing disease can be characterized by the opaque musculature in the tail of affected shrimp. Going by the technical name "spontaneous necrosis," this progressive disease begins as a whitish area usually near the end or middle of the tail. Caused by an adverse stress such as low oxygen concentration or rapid change of the water's temperature or salinity, the condition progressively worsens, leading to death unless the harsh conditions improve. The disease may occur frequently in shrimp held in bait holding tanks and could be confused with cotton shrimp unless shrimp with each of the two conditions could be compared.

The above necrosis* is reversible. Shrimp provided water of adequate quality will lose the opaque appearance unless the condition has developed beyond a certain threshold point. Once the tip of the tail acquires a totally chalky white appearance, the shrimp usually dies. The really amazing phenomenon that biologists should pursue is how shrimp with a partially necrotic condition can, within a day or so, recover and appear normal. Microscopic examination of affected opaque tissue reveals nearly totally dissociated material, but a few days later, the tissue appears to regain its normal

character. Investigation of this regenerating tissue aided by the electron microscope should go a long way to explain the process of muscle regeneration, a transformation that takes considerable time in man and other vertebrates.

Another condition called "cramped shrimp" develops in individuals held in bait tanks and ponds. The tail can be completely or partially flexed. It becomes so rigid that it cannot be straightened out. Partially-cramped individuals swim about in a humped fashion and may survive the ordeal. Those laying on their sides seldom improve and usually die. An imbalance of ions appears to cause cramping.

Occasionally a shrimp portrays a golden appearance throughout all its tissue. The yellowish-gold shrimp may appear either opaque or transparent, and the rarity of affected individuals reared in ponds suggests that the condition may represent an hereditary phenomenon rather than one resulting from dietary deficiency or some other unnatural process.

The crab leech may also occur on penaeids, but not nearly as frequently as it utilizes the crab or grass shrimp.

A variety of symbionts and fouling organisms often attach to older shrimp. Usually those shrimp not molting for long periods reveal the most spectacular cases because large sessile barnacles grow on the carapace or elsewhere. Algae, hydroids, and occasionally other organisms attach to and sometimes invade gills, eyes, or less vulnerable regions. Presumably these interfere with the best possible life style for a shrimp.

Confusion may also exist when separating parasites from normal anatomical structures. One of these structures, the pod-like sperm capsule, or spermatophore, is rarely seen in inshore shrimp. Most individuals spawn offshore. During mating, the male transfers his sperm capsule to the female where it becomes attached to the female's external genital organ (thelycum), located between her fourth and fifth pair of walking legs, by means of various anchoring devices and a glutinous material. Since the brown shrimp has a closed thelycum, copulation apparently occurs between a recently molted, soft-shelled female and a hard-shelled male in contrast with the process in white shrimp which takes place between hard-shelled individuals because the thelycum is open. In spite of the plates, bristles, spines, glue, and other devices, the capsule easily dislodges. Nevertheless, fertilization of ova in these individuals seems to take place.

The female white shrimp with the attached spermatophore in Figures 73 and 74 shows a typical condition in offshore shrimp. A fisherman, however, collected this particular shrimp from inshore water where attachment is rare and, for that matter, unproductive if eggs are released unless the salinity concentration is higher than normal. The strange attached object could be misinterpreted as an external parasite.

Some noninfectious diseases result from

Figures 73 and 74. A male's spermatophore (encapsulated sperm) attached to a 173 mm long female white shrimp. Top, side view. Bottom, underside view.

environmental contaminants. Usually definite proof for such relationships is lacking and that is the case for a growth that appears to result from some unidentified pollutant in Ocean Springs, Mississippi. An overgrowth of muscle protruded through the ventral portion of the last abdominal segment in both post-larval brown and white shrimps (Figures 75 to 77).

Figures 75-77. Abnormality in postlarval brown shrimp. Top, fourth through sixth tail segments of a normal shrimp. Middle, moderate overgrowth of muscle tissue extruding through joint of sixth segment. Bottom, slightly larger shrimp (13 mm) with frayed overgrowth. The likelihood exists that the growth (hamartoma) resulted from an unidentified pollutant interfering with the normal growth process of the shrimp.

Even though many thousand shrimps were examined from a variety of habitats, only postlarval individuals from near a small boat harbor receiving the city's treated sewage, the presumed most polluted habitat, exhibited the anomaly. Apparently something interrupted the normal growth process. When postlarval shrimp grow from 6 to 25 mm in length, the relative length of the sixth abdominal segment gradually decreases. In affected shrimp, the muscle apparently continued to grow at the previous rate while the relative length of exoskeleton decreased as expected for normal shrimp. As a result, the muscle folded and protruded through a weak joint, usually pushing the ventral nerve cord with it. Since the nerve is stretched and vulnerable to being frayed by mud and sand, the affected shrimp probably cannot avoid predators before reaching adulthood because shrimp avoid predators by darting backwards using quick flexions of the tail.

GRASS SHRIMP

Even though not commercial species, grass shrimps (especially *Palaemonetes pugio*) deserve inclusion in the treatment on shrimp diseases because they are usually easier than penaeids to obtain with a dip net, they are better hosts for a few of the same or related symbionts that associate with penaeids, and one of their isopod parasites often attracts a variety of queries. Also, they act as a very important source of food for fishes, birds, and other animals.

Near banks of bayous and among marsh grass, thousands of specimens of *Palaemonetes pugio* can often be seined or dip netted in a few minutes. An adult cannot grow as long as a regular house-key and can quickly be separated from young penaeids because the female broods her eggs under her abdomen. A few grass shrimp symbionts will be discussed; the cover-illustration reproduced as Figure 78 shows several of these.

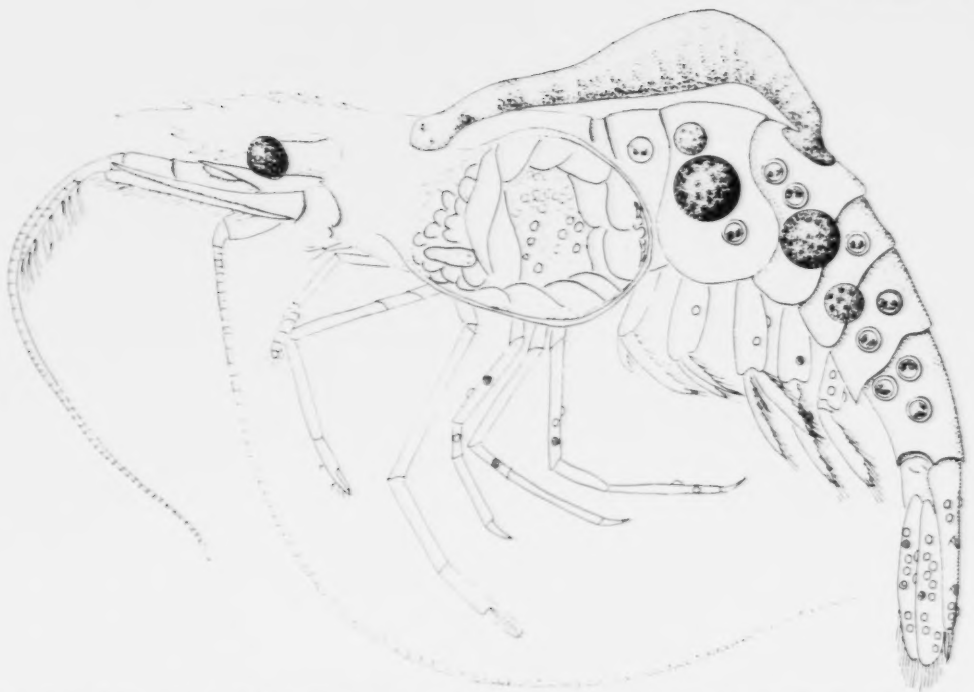


Figure 78. A grass shrimp *(Palaemonetes pugio)* with a variety of its symbionts. On the tail fan and legs, a ciliate *(Lagenophrys lunatus)* lives within a transparent encasement opened to the external environment. Another ciliate attached by its stalks to the anterior claw. In the tail muscle, the encysted spherical fluke larva *(Microphallus choanophallus)* looks conspicuous in the illustration and also in the living shrimp if a host is held up to the light. The three larger dark spheres constitute the same fluke cysts, but hyperparasitized by a haplosporidan protozoan *(Urosporidium crescens)*. When infecting a related fluke in the blue crab, the association has been termed "buckshot" or "pepper spot." A bopyrid isopod *(Probopyrus pandalicola)* occludes the anterior side of the shrimp, and the common leech *(Myzobdella lugubris)* darts about on the top of the shrimp. The text covers these and several other symbionts from the grass shrimp.

Protozoans

The loricate ciliate *(Lagenophrys lunatus)* encased on the tail fan, walking legs, and swimming legs in the illustrated shrimp provides an easier model to study than the related ciliate species infesting the gills of the blue crab. It can be observed without harming the host and its development on a molting host can be followed. This protozoan species appears specific to shrimps of the family Palaemonidae (grass and river shrimp) in fresh and brackish water.

Within the transparent lorica*, the peritrich projects its oral cilia through the aperture for feeding on scraps from the host's food and on phytoplankton. Even though its body is attached to the opening of the lorica, a gap exists that allows a swarmer (its telotroch larva) to emerge. The adult organism can also contract, sealing off that aperture formed by the lorica's flexible collar extension. Microscopic examination clearly shows the horseshoe-shaped macronucleus and small micronucleus diagnostic of many ciliates.

Preceding the host's molting, the organism, most prevalent on sites with the greatest water flow, undergoes a special type of asexual division producing two swarmers (free swimming larvae). Loricas on fresh molts contain these swarmers, as well as dividing (asexually reproducing), trophic (feeding), and conjugating (sexually reproducing) individuals. In other words, when the host molts, stages have already

been produced to reinfest the same host or additional hosts and thereby perpetuate the species.

Other ciliates also infest grass shrimp. One (*Terebrospira chattoni*) can be seen almost anywhere except on or adjacent to the gills. Small (50 to 100 μ) elliptical cysts usually divided into compartmentalized sectors may contain individuals or be empty. Related apostomes feed on molting (exuvial) fluid, but this species has become adapted to feeding on the endocuticle. The tiny flattened ciliate can be found digesting the cuticle* at the end of a tunnel leading away from one of the empty compartments. Is this a transition between an external and internal symbiont?

In addition to ciliates, a variety of microsporidan protozoans also infect grass shrimp. One (*Pleistophora lintoni*) differs little from related species in penaeids, crabs, and even fishes. Large numbers of spores fill the pansporoblast's chamber (Figure 79), and a heavy infection produces an opaque tail characteristic of "cotton shrimp."

Another species (*Inodosporus spraguei*) produces the same gross appearance, but the spores are unusual. Each undischarged spore (with polar filament intact) contains three or four long extensions ("tails") on its basal portion and a divided short one on the apical end. After an infected shrimp is eaten, tails on a spore voided with the predator's feces probably aid in tangling the spore to vegetation or trapping tidbits that might ultimately induce another grass shrimp to ingest it. While developing, the tails may channelize nutrients and ions to and from the forming spore. Eight of these tailed spores occur within a pansporoblast.

Electron micrographs (Figures 80 and 81) show the organelles that these tiny (3 μ long by 2 μ wide) spores possess. The polar filament has its base (end of the diagonal narrow structure) attached to the apical end. Alterations in the plug at this juncture allow the tube to turn inside out and extrude a considerable distance (about 40 μ). The process is aided by the lamellar (layered) structure (polarplast) at the apical end. The small, round, peripheral structures are cross-sections of the uneverted coiled portion of the filament. The external tails do not extrude; they develop simultaneously with the spores. The second micrograph shows several early developing stages separated from mature ones by some unharmed host muscle tissue. Each of the early stages will divide, producing eight spores. The tunnel-like arrangements adjacent to the maturing spores constitute various sections through the tails. Luck allowed a few spores in this very thin section to reveal the place where the tails join the spores.

Whereas microphallid larval cysts (metacercariae) are hard to see in the penaeids because of a shrimp's large size and the paucity of infections, cysts of *Microphallus choanophallus* are seldom absent in most stocks of *Palaemonetes pugio*. By holding a grass shrimp up to a light or to the sky, many opaque specks, each representing a cyst, stand out conspicuously. Often, *Urosporidium crescens* hyperparasitizes* one or more of the cysts (Figure 78), making the cyst even more recognizable.

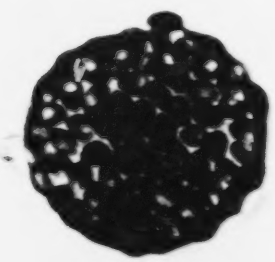


Figure 79. A microsporidan (*Pleistophora lintoni*) from the tail of the grass shrimp. Members of this genus have several to many hundred spores per chamber.

Metazoans

A bopyrid isopod (related to terrestrial organisms called sowbugs, roly-poly bugs, or potato bugs) stands as a good example of a parasite on grass shrimp that is not found

Figures 80 and 81. Electron micrographs of a microsporidan *(Inodosporus sprague)* from the grass shrimp. Top, close-up of spore that causes cotton shrimp. Large light-colored round objects near periphery and straight object diagonal through spore all portray different views of the filament that protrudes and discharges infective material. Bottom, mature spores on top and developing ones on bottom are separated by functional muscle tissue in between. The common species in the blue crab *(Ameson michaelis)* and some other microsporidans destroy adjacent muscle tissue. Eight spores occur within a membrane for the figured species. Members of the genus are unusual because they have long external tails attached to the spores. The tubular material among the spores are these tails. Inspection of either photo will reveal where some of the tails attach. They probably act as a means to provide nutrients to developing spores and attach free spores to vegetation or debris so that the spores can be eaten.

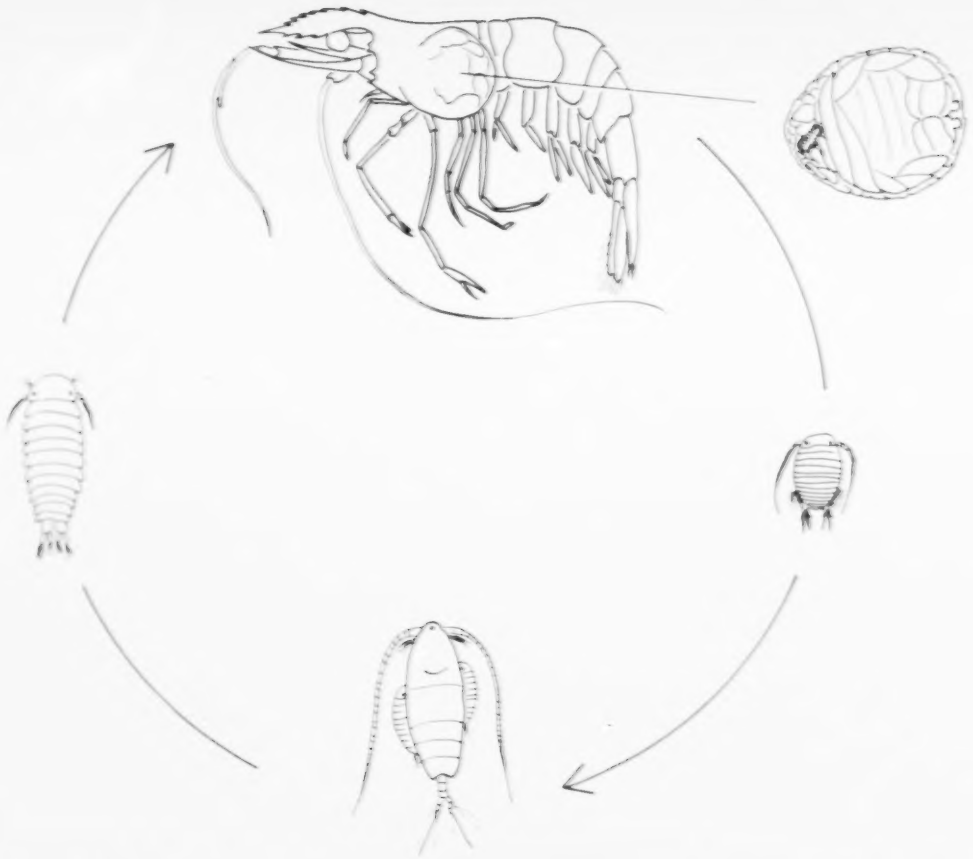


Figure 82. Life cycle of a bopyrid isopod *(Probopyrus pandalicola)* under the carapace of the grass shrimp. The tiny male clinging to the illustrated female separated from the host fertilizes the ova, and several individuals of the resulting larva remain with the female until that larva develops and the host molts. Once freed, the larva attaches to a copepod host and develops further into the stage infective for grass shrimp.

on local penaeids. The coloration and large swelling on the side of the carapace make an infested individual obvious. Different species of bopyrids infest various crustaceans; the one on the grass shrimp *(Probopyrus pandalicola)* associates only with specific grass and river shrimps. As suggested by Figure 82, it undergoes a life cycle requiring an intermediate host*.

The large, distorted female isopod nearly usurps the host's entire gill (branchial) chamber (Figure 83). The ventral (underside) view of the female shows the dwarf mature male near the posterior end among the female's pleopods. She broods many larvae within her marsupium (middle portion of illustrated female). When the host molts, many individuals of the first stage larva (epicaridean) are liberated and swim toward light. After attaching to the copepod intermediate host *(Acartia tonsa)*, the larva metamorphoses into another larval stage (microniscus) larva which grows rapidly at the expense of the copepod, and, when several are present, may even surpass the host-copepod's mass. That larva molts to form the larva (cryptoniscus) infective for either a larval or young grass shrimp. The first individual reaching a host's gill chamber develops into a female, whereas all later ones become males. If the ability for sex transformation is the same as for a related bopyrid, a male taken from one grass shrimp and introduced to an uninfested shrimp

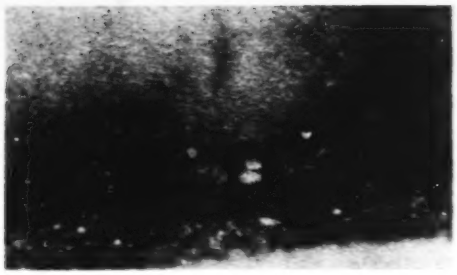


Figure 83. Adult female bopyrid isopod (*Probopyrus pandalicola*) under carapace of grass shrimp.

Figure 84. Three individuals of a common leech (*Myzobdella lugubris*) swaying about on their grass shrimp host.

would turn into a female! If several larvae invade an uninfected shrimp simultaneously, all become females, but only one would eventually mature. Think of the experiments that could be conducted using this host-symbiont system.

The ability for symbionts and hosts to sense their surroundings provides a continual source of problems to investigate. The grass shrimp acts as a good host to study for harboring the "crab leech" *(Myzobdella lugubris)*. Occasionally one finds an individual with two or more leeches attached (Figure 84). However, if a person puts an infested and many noninfested shrimp in a bowl and starts adding leeches to the bowl, he will observe that most will eventually attach to one or a few shrimp. As many as 20 can reside on a single shrimp.

The leech probably does not utilize the shrimp as much as the blue crab for deposition of cocoons. It will use the shrimp, though, and after it does, the shrimp often eats the leech. Perhaps this results from lethargy on the part of the spent• leech. I have seen the anterior third of an eaten leech remain alive in a grass shrimp for an entire day, sucking on the digestive gland and moving. The shrimp stayed alive!

A few freshwater crustaceans rate highly with consumers or fishermen, and they harbor a variety of parasites. One of these parasites from a crayfish will serve as an example.

Cats and other mammals that feed on crayfish (pronounced "crawfish" in Louisiana) from ditches may acquire a lung fluke *(Paragonimus kellicotti)*. Figure 85 shows the closely related oriental lung fluke of man *(Paragonimus westermani)* trans-

Figure 85. The oriental lung fluke (*Paragonimus westermani*) which is related to one that encysts in pairs in the lungs of local carnivores that feed on crayfish.

mitted by a few crabs in the Far East. Unlike many intestinal flukes that infect local estuarine and terrestrial mammals, the local lung fluke can grow over 1 cm in length. It has provocative mate-finding behavior that needs to be critically investigated. Nevertheless, if two or occasionally more individual migrating larvae occur in the cat, they quickly join together and become encapsulated by the host in the lung without causing much harm. On the other hand, if a single worm infects a cat, it migrates about for an extended period in the lung or lung cavity, presumably needing to come in contact with a mate and occasionally causing

continuous damage to the host. Thus, a host appears better off with several worms than with one. Like most investigated digeneans, *Paragonimus kellicotti* appears to cross-fertilize rather than fertilize itself.

According to veterinarians along the Gulf Coast, this freshwater lung fluke is rare in pets except for outbreaks in Mobile, Alabama. Still, presence of the fluke should be recognized. Pets that eat either dead or living fish from the estuaries stand the chance of acquiring several different helminths.

VERTEBRATES AS HOSTS

FISHES

Because of the large number of fishes• present in the northern Gulf, I make no attempt to treat each species as thoroughly as I covered symbionts of selected invertebrates. I picked only a few of the many invertebrates from the Gulf, but they are all commercially important. A much larger number of commercially important finfishes than shellfishes inhabits that region. The number of fishes one is likely to encounter commonly while shrimping and fishing probably would be about 100, but exerted effort should probably turn up over 400 species. These fishes exhibit a wide variety of living and eating habits. Such ecological differences plus additional biochemical and physiological ones guarantee a variety of parasites.

In our Parasitology Section at the Gulf Coast Research Laboratory, one of our investigations deals specifically with various aspects of parasites from the Atlantic croaker. From this single species in Mississippi, we have encountered about 90 different species of parasites, about one-third of which occur commonly. Wide overlap of different hosts occurs for some species infecting croaker, whereas others infect only the croaker or just a few host species.

Possibly a remark should be added for those squeamish about parasites from fish in general. When one cleans a fish, he removes most of the parasites. Those that remain in the flesh or under the skin may be either easily visible or too small to see with unaided eyes. In either case, most do not infect man, but those that can die readily when cooked, even for short periods.

The following treatments should encourage an appreciation of some of these variously-adapted piscine symbionts. Most will be grouped by category of symbiont. The reader, however, should remember that many parasites utilize more than just a fish to complete their life histories, and some of those hosts have already been discussed. In order to help readers locate the site of a parasite, Figure 86 reveals many anatomical features of a bony fish in general and of the Atlantic croaker specifically. Because many symbionts from elasmobranchs do not involve bony fishes (teleosts) and because Hollywood has spurred recent interest in sharks, elasmobranchs deserve some special comments.

About 800 species of elasmobranchs (sharks, skates, and rays) exist worldwide. Of these, at least 38 may occur during a part of the year in the northern Gulf of Mexico and 26 are sharks. Many sharks can be caught near shore until the water temperature drops. Perhaps their prey moves offshore or becomes otherwise unavailable during winter. The bull shark, a common species, exemplifies this by not turning up in nets or on fishermen's long lines• in Pensacola, Florida, from November to mid-April. Sharks often aggravate both commercial and recreational fishermen by damaging fishing gear and removing bait intended for other fishes. However, because sharks are usually available, because of the thrill of catching a shark, and because sharks taste good, many are caught and brought ashore.

Different elasmobranchs feed on a variety of fishes and invertebrates, including many commercial species. This variation among species is reflected by the variety of internal parasites they host. Large sharks tend to have more individual specimens than stingrays, but the large rays, probably because they feed on a wider range of dietary items than sharks, including crustaceans and molluscans in addition to fish, usually host a larger number of species.

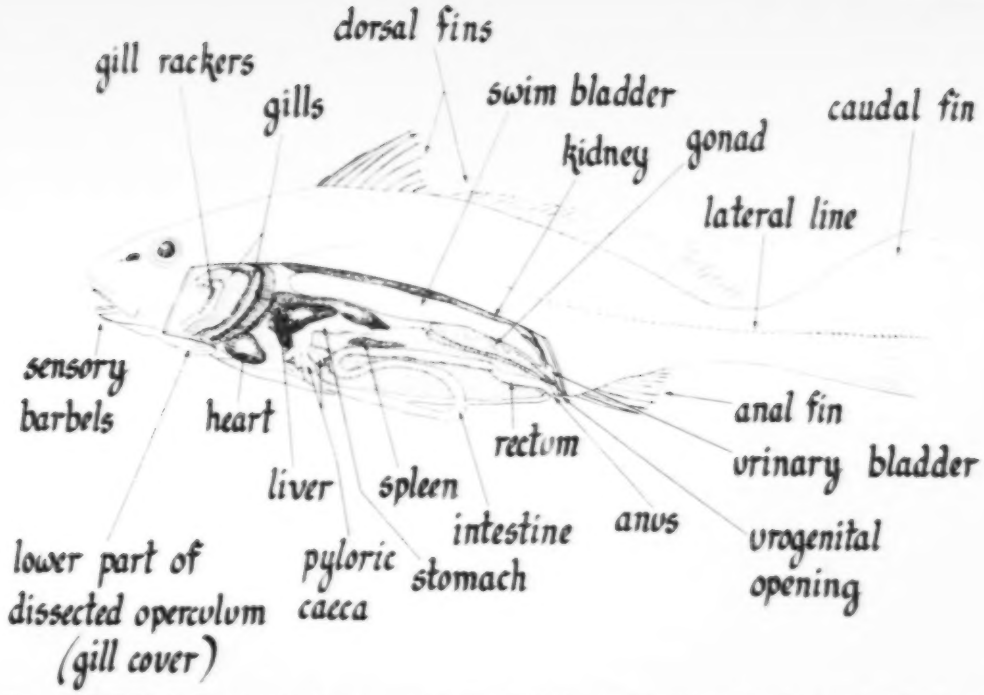


Figure 86. Selected anatomical features of a bony fish (Atlantic croaker). Most fishes have similar, but modified, features.

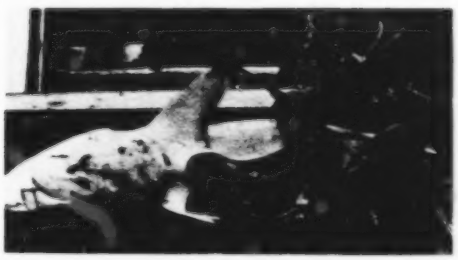


Figure 87. Opening up the spiral valve of a small blacktip shark. This modified intestine increases the amount of absorptive area and provides an ideal habitat for tapeworms.

Many species of parasites, especially tapeworms, occur in one or a few species of elasmobranchs. This specificity may relate primarily to the kind of prey preferred by the different hosts. Structures of the jaw and teeth usually govern the type of prey an elasmobranch can easily capture. Sharks with sharp, pointed, or serrated teeth (charcharhinids) probably eat many fish, whereas sharks with flattened or small teeth (mustelids and squalids) eat more crustaceans and molluscs. Modifications of the gut also have some bearing on the attachment organs of worms and therefore on the species of parasites present. Rather than possessing a simple tube for an intestine like most teleosts, elasmobranchs have developed a spiral valve which increases the absorptive area. This structure exists in a few different forms. The concentric spiral valve in charcharhinid sharks (Figure 87) reminds me of a jelly roll whereas that in skates, rays, and other sharks looks more like a corkscrew.

Microbes

Lymphocystis exemplifies a viral disease of fishes which has external signs* that can be readily observed (Figure 88). A specific type of host cell (fibroblast*) becomes infected by the viral particles and may enlarge (hypertrophy) to a few hundred times its original size. Enlarged cells acquire a thick hyaline* capsule, and critical examination of an affected fish will reveal these individual cells among crusty masses, or "tumorous growths." The disease cannot be associated with cancer* (see tumor in

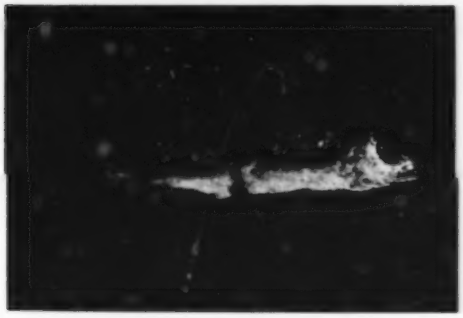


Figure 88. Atlantic croaker with lymphocystis. White encrusting masses consist of numerous greatly-enlarged connective tissue cells infected with a virus.

glossary) in the true sense because the giant-sized cells do not divide nor metastasize. In fact, the disease rarely kills its host outright, but probably does make it vulnerable to predation.

In Mississippi Sound, two strains of the lymphocystis-virus cause disease in estuarine fishes. Several other strains infect other fishes in adjacent and distant waters, but for purposes of showing that strains differ, I will limit my discussion to a strain which affects the Atlantic croaker and sand seatrout and another which affects the silver perch. One or two fishes other than those mentioned can be experimentally infected with each strain, but the croaker strain will not infect the perch and vice versa. Development of infections in croaker progresses more slowly at low temperatures, but infections occur in local water most prevalently during cold months. Granular masses can cover portions or nearly all of the skin and fins and can slough off in older infections. Once the encrusting masses slough, the host appears resistant to a challenge infection.

As indicated above, the strain in silver perch does not infect the croaker, and the viral particle measures larger than the one from croaker. Figure 89 shows an electron micrograph of the virus particles. Even though the perch's body surface exhibits crusty masses (Figure 90), infections also occur commonly in the gills (Figure 91) and in various internal organs. Figures 92 and 93 reveal an infection involving the eye! Perhaps the virus invades internally because a symbiotic isopod *(Lironeca ovalis)* produces a lesion on the gill, allowing it to spread through the blood stream (Figure 91). The isopod commonly occurs on perch with lymphocystis in the gills as well as on several other fishes, none of which exhibits lymphocystis.

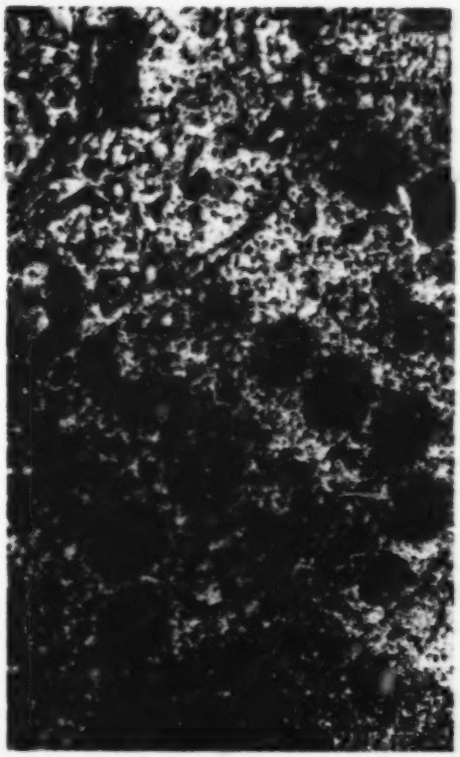


Figure 89. Electron micrograph of lymphocystis virus particles (dark hexagon-shaped structures) in an enlarged connective tissue cell from an Atlantic croaker. The granular-like structure at the bottom is a characteristic nonrefractile inclusion body (compare with refractile inclusion bodies associated with a virus in penaeid shrimp).

Lymphocystis in croaker from Mississippi may be related to increased pollution or other stresses. Long-time sports fishermen who have fished croaker from Mississippi Sound for decades have witnessed their first cases of lymphocystis during the past few years. Additionally, I have seen a considerable increase in prevalence* since 1969 in Mississippi waters. In fact, occasionally over one half of a hundred croaker in a trawl haul will have recognizable hypertrophied cells. The disease in perch also can infect over half a

Figures 90 and 91. Silver perch with lymphocystis. Left, infection similar in appearance to that from Atlantic croaker. Right, raised operculum showing infected gills and isopod *(Lironeca ovalis)* that may allow dispersal of the infective agent to the internal organs. Croaker have no apparent internal (visceral) infections.

Figures 92 and 93. Pop-eye caused by lymphocystis infection below and behind the eye. Top, side view showing enlarged individual cells massed together with rich blood supply. Bottom, top view of same fish showing extent of bulging eye.

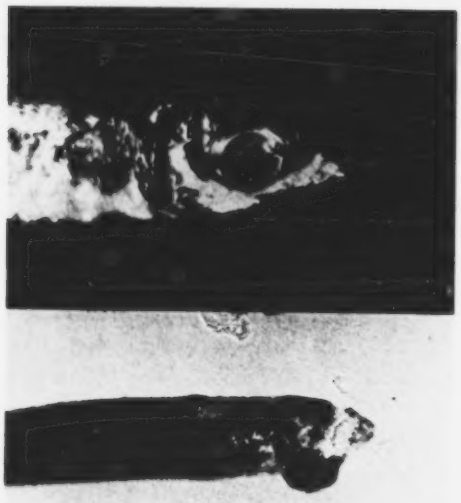
sample, but the prevalence of infections fluctuates differently than that for the strain from croaker. Possibly fluctuations relate to the amount of rainfall, increasing with abundant rains.

Several other viral organisms probably infect Gulf fishes, but few have been reported. Considerable research needs to be conducted on both viral and bacterial diseases.

Even though bacteria can be more easily studied than most viruses, relatively few species from marine fishes have been carefully investigated. A chronic fish-kill, one that occurred over a long period of time in Alabama and northwestern Florida, appeared to be caused by the combined effects of bacterial involvement and environmental stress. Without stress-factors in addition to bacteria, the bacteria by themselves seldom cause fish mortalities.

"Fin rot syndrome," a condition for which the rays of fins exhibit erosion, disintegration, fusion, or abrasion, usually with associated bleeding (hemorrhaging), can be associated with bacteria and can result in death. In some regions heavily contaminated with industrial and agricultural pollutants, however, bacteria are not always involved in cases of this syndrome. As with the term "cancer," the name "fin rot syndrome" also applies to more than one specific disease. In Mississippi, lesions on many fish probably result predominantly from predators and trawl damage in conjunction with trauma caused by contaminants and other environmental stresses.

Similar to situations with most disease-causing agents, a relatively small number of bacteria may occur without harming the host. After undergoing stress, however, the host's defense mechanisms allow the bacterium or combination of contagions to multiply rapidly and thereby harm it. An example of a secondary bacterial infection associated with a protozoan (*Epistylis* sp.)



Figures 94 and 95. Tidewater silverside with gas bubble disease. Top, side view. Bottom, top view emphasizing bulging nature of eye and clearer view of a bubble. A variety of factors cause pop-eye and some are discussed in the text.

will be discussed in the section on protozoans.

In most bacterial diseases, the presence of bacteria has to be determined by culturing in order to diagnose a disease. The nonspecific "pop-eye" disease (technically called "exophthalmos") provides a good example. A variety of bacteria can cause this disease recognizable by a bulging eye. We, however, have already learned that lymphocystis can cause eyes to bulge in silver perch, and many other factors also cause a protrusion. Helminths cause it and so can mechanical injury or gas bubbles. A case of "gas bubble" disease in a tidewater silverside is illustrated by both top (dorsal) and side (lateral) views (Figures 94 and 95). The presence of gas does not rule out bacteria, but gas can be produced by overaeration, malfunctioning organs, and other causes. Because bacteria in finfishes that could influence human health are the same as those in shellfishes, fish from contaminated waters should also be cooked to insure a safe product.

Protozoans in General

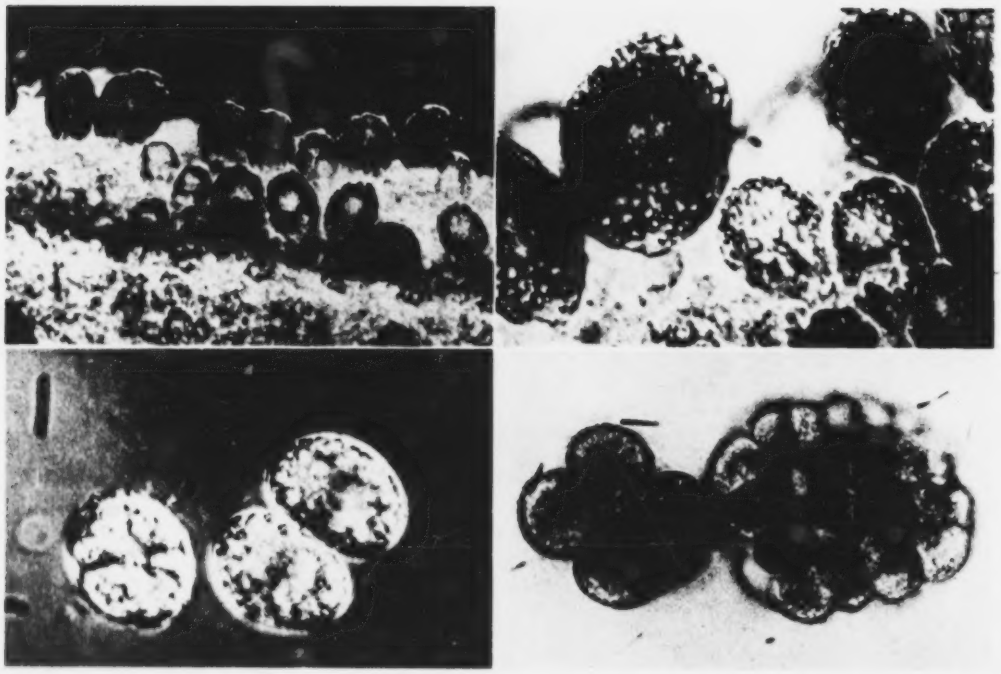
Many different groups of protozoans infect fishes. The phylum* Protozoa by definition contains all single-celled animals, both parasitic and entirely free-living. Actually, many biologists presently working with different nonrelated protozoans have decided that they should split up the phylum into several phyla, thereby further emphasizing the differences among nonrelated groups. Not until various stages of selected species can be critically investigated with an electron microscope and modern biochemical analyses, can many scientists feel confident about the classification schemes. Many relationships still need clarification.

Even though single-celled, protozoans possess a variety of specialized structures that aid in food gathering, locomotion, attachment, and protection. Some of these structures will become apparent in the following sections. The sections also present a few of the numerous possible examples which portray a wide range in fish-symbiont relationships. They include flagellates, amoebas, sporozoans, microsporidans, myxosporidans, and ciliates.

Flagellates

A dinoflagellate acts as the most harmful flagellate to captive marine fishes. Most dinoflagellates occur in the plankton*, possess chlorophyll*, and do not parasitize hosts; they possess two flagella (read later comments on cilia) which permit the tiny organism to spiral through the water. One wraps around a subequatorial depression of the subspherical organism and the other trails a long distance posteriorly. Actually, the parasitic species also produce a stage that looks like a typical planktonic dinoflagellate mentioned above, and it is that stage that allows proper classification of the parasite. That stage, however, turns into opaque chalky blobs (Figures 96 and 97) on the gills and skin of fishes.

A few different species of parasitic dinoflagellates occur in the Gulf of Mexico, but one *(Amyloodinium ocellatum)* happens to be especially pathogenic to captive fish. Careful examination reveals a large nucleus, several food vacuoles, an



Figures 96-99. A parasitic dinoflagellate *(Amyloodinium ocellatum)* from the gills of a fish. Top left, a moderately-heavy infestation of feeding individuals (trophonts) on the gills. Top right, close-up showing food vacuoles, nucleus, attachment structure, and pigment stigma (above attachment). Bottom left, encysted individual undergoing early divisions. Bottom right, later division stages. From one trophont develops 128 cells that each form two swimming dinoflagellate-swarmers. Each swarmer can infect a fish, repeat the cycle, and kill the fish if enough individuals infest it.

attachment plate with numerous projections (rhyzoids) that penetrate the host-tissue, an elongated flexible process (stomapode tube) that apparently aids in digesting host-tissue, and a reddish sensory organelle near the attachment (Figure 97). Other features require an ultrastructural examination to distinguish them.

Rapid and extensive multiplication allows the parasite to harm confined hosts. Once the attached feeding stage (trophont) on the gills reaches a large size (barely visible with an unaided eye) or the host becomes severely stressed, the parasite withdraws its penetrating processes, drops to the substratum, and covers itself with a cellulose secretion. Cellular division (Figures 98 and 99) continues until 128 resulting cells develop into the greenish chloroplast*-abundant, free-swimming, swarming cells (dinospores). The dinospores then divide once to form a total of 256 swarmers all originating from the single attached trophont; each can infest a host and develop into a trophont. In the natural environment, contact between swarmer and fish seldom occurs, but in an aquarium or pond, the probability of contact is high. When thousands of these individuals infest one fish (Figure 96 shows a moderate infestation on the gills), the host can die within half a day, and nearly all marine fishes are susceptible.

Freshwater baths given aquarium-fishes will cause the parasites to drop off the gills, but a few of these can get caught in mucus or be swallowed to remain dormant in a host's intestine. They can reproduce in water with from 3 to 45 ppt salt, and just one individual can start new infestations. Infestations represent an enormous loss to marine aquaculture and the aquarium trade. A freshwater species that more readily infests the skin rather than the gills also kills many fish.

Other types of flagellates also infect the gills, skin, and gut of estuarine and marine fishes. Those that infect fishes possess from

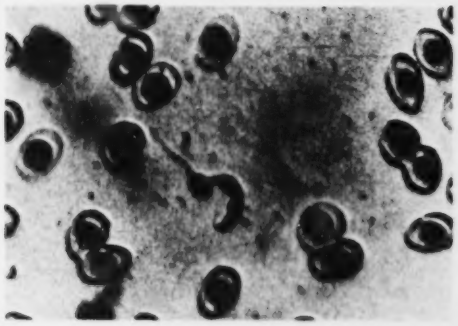


Figure 100. Trypanosome *(Trypanoplasma bullocki)* in blood of the southern flounder. Note the anterior and posterior flagella. Also, note that fish red blood cells, unlike human ones, have nuclei.

one to eight flagella. Most occur in low numbers in fish from natural waters, but can rapidly intensify in stressed or cultivated hosts. For most of those flagellates, the identification and life histories are poorly understood, but reproduction typically takes place on the host.

The blood of several fishes harbors a different type of flagellate. The most common blood flagellate in Mississippi estuaries (*Trypanoplasma bullocki*, Figure 100) has two flagella, whereas some others have one. Both flagella extending from this elongated organism originate at its anterior end. One borders a protruding undulating membrane and trails beyond it. This parasite, the body of which is longer than the host's blood cells, can best be appreciated when viewed alive. A drop of blood from an infected southern flounder placed under a coverslip reveals intense undulating activity through a microscope. If a fish has trypanosomes, individuals can be observed easily by allowing several drops of blood to clot. The parasites swim about in the clear serum*.

Unlike their mammalian counterparts which cause African sleeping-sickness, piscine trypanosomes rarely cause disease. One species has harmed hatchery-reared rainbow trout in California.

Transmission of trypanosomes into fish occurs when leeches obtain their blood meal. In the case of *Trypanoplasma bullocki* in the southern flounder, sexual reproduction of the flagellate probably takes place in a specific small leech (*Calliobdella vivida*). In addition to being an invertebrate host, a leech can also be a passive vector* for trypanosomes.

Amoebas

Commensal amoebas probably occur in intestines of Gulf fishes, but fishes have not been adequately examined for them. At least one species has invaded pond-reared freshwater fish in the southeastern U.S. and caused serious disease. Implicated mortalities may have required additional involvement with bacteria or other protozoans.

Sporozoans

A group of entirely parasitic protozoans called Sporozoa have members that typically have a spore* stage. Life cycles usually include alternation between one host in which gametes* and asexually-produced individuals are formed, and another host in which gametes unite and spores with infective stages develop. Malaria-causing organisms belong to this group; fertilization and "spore" (nonresistant) formation occurs in mosquitoes, and the asexual phase takes place in reptiles, birds, man, and other mammals.

Coccidians constitute the most studied organisms with "resistant" spores (those that can withstand the elements when passing from one host to another) because of their devastating effects on poultry and livestock. Some species have intermediate hosts, whereas others bypass such hosts completely and are transmitted by feeding on the spores. Figure 101 shows four spores in a cyst (oocyst) taken from a lesion on the tail fin of a Gulf killifish in a Louisiana marsh in Cameron Parish. Each spore contains two organisms (sporozoites) presumably infective for other killifish. The number of spores and sporozoites per cyst determines to what genus a species belongs. The genus of the figured species (*Eimeria* sp.) also includes many species that infect most farm-animals; however, its cyst wall is thinner because the host's aquatic environment is seldom threatened

Figure 101. Coccidian (*Eimeria* sp.) from lesion on tail fin of the Gulf killifish. Each thin-walled cyst contains four spores, and each spore contains two infective organisms (sporozoites). Related members of this same genus cause serious economic losses to untreated, infected, farm animals.

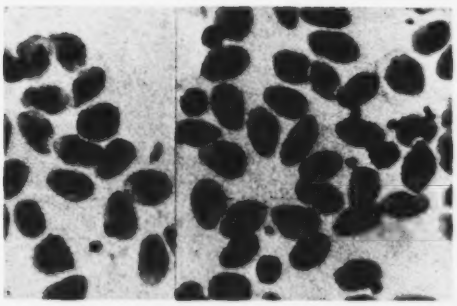


Figure 102. Hemogregarine (*Haemogregarina platessae*) in blood cells of southern flounder. Note that the parasite (a gamete stage) is inside the red blood cell rather than external to it. A pair of gametes fuse to form a zygote, presumably in a leech.

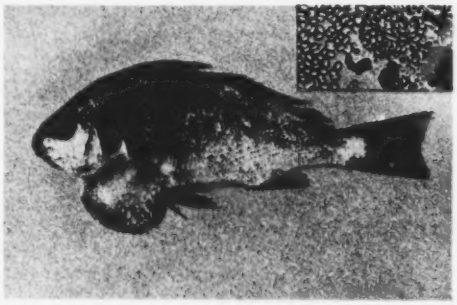


Figure 103. Spot with tumorous growths caused by a microsporidan protozoan (*Pleistophora* sp.). Insert shows microscopic view of spores.

by desiccation. Unlike species in most warm-blooded vertebrates, all or most of those infecting fishes produce infective stages while still in fish tissues and do not utilize an intermediate host.

Different piscine coccidians involve different host tissues such as the testes of menhaden and swim (air) bladder of cod. Medical doctors have misdiagnosed as human coccidian infections cases where cysts were recovered in stools of people having eaten sardines and other fishes uncooked. These fish parasites do not harm man.

Related sporozoans (hemogregarines) infect peripheral red blood corpuscles of elasmobranchs and bony fishes. Most species presumably also infect blood cells in bone marrow, liver, or elsewhere in the same host, but these stages have not been properly described for a piscine hemogregarine; they have been for a turtle species. For some other species, however, asexual multiplication occurs in peripheral blood. More prevalent in Mississippi fishes than trypanosomes, hemogregarines may be more difficult to find in a cursory examination because thin blood smears must be stained to observe the subspherical to greatly-elongated parasites (gametes*) which occupy a peripheral blood cell (Figure 102). An individual southern flounder may have both a hemogregarine (*Haemogregarina platessae*) and a flagellate (*Trypanoplasma bullocki*). The same leech probably transmits both parasites. Blood-feeders other than leeches may also transmit some hemogregarines.

Microsporidans

Another group of Protozoa, the Microsporida, has been treated in some detail earlier when discussing the life cycle of *Ameson michaelis* in the blue crab and the spores of *Inodosporus spraguei* in grass shrimp. Several microsporidans infect fishes, but more appear to infect species in regions more temperate than the northern Gulf. In the Northeast, winter flounder and shad are conspicuous hosts. In the Gulf, sciaenids (the croaker, spot, drums, and seatrouts) and a few other fishes host microsporidans, but cysts are usually small and infections are much more prevalent in crustaceans and other invertebrates, including flukes. The conspicuous growth

Figure 104. Myxosporidan from cyst in liver of striped mullet showing discharged polar filaments.

on the spot in Figure 103 results from large masses of a microsporidan (*Pleistophora* sp.). Some growths are hard, whereas others are soft; all are infrequently seen.

Myxosporidans

Myxosporidans occur much more commonly than microsporidans in Gulf fishes, and they comprise a quite unusual protozoan group for several reasons. From an evolutionary point of view, Myxosporida does not fit in with other protozoan groups because members have more than a single cell. Depending on the species under consideration, the actual number of cells per spore differs, but a spore of most piscine species develops from five cells.

From an anatomical point of view, myxosporidans possess internal polar capsules which evert an elongated filament (Figure 104) similarly to the various structures (stinging, adhesive, anchoring, and entangling) everted from capsules found in jellyfishes and other cnidarians.

From a host-symbiont point of view, myxosporidans can be divided into two primary types: those that infect lumens of hollow organs such as the gall bladder (coelozoic) and those that infect tissues such as muscles (histozoic). Rather than occurring in spaces between muscle cells like a histozoic form in the strict sense, some species develop within muscle fibers (cytozoic).

Tumorous* growths caused by a histozoic myxosporidan *(Myxobolus lintoni)* provide a dramatic example (Figure 105). Not prevalent in the Gulf, the disease, which

Figure 105. Sheepshead minnow with tumorous growths caused by myxosporidan *(Myxobolus lintoni)*. As in the microsporidan infection from spot, the cysts contain millions of infective spores.

affects the sheepshead minnow at least from Mississippi to Texas, may be related to pollution or other stresses. It has other similarities to cancer in addition to possibly being induced by a pollutant. Vegetative growths invade and replace healthy muscle tissue and new growths spread to other regions of the body. A related species *(Myxobolus cerebralis)* invades and erodes cartilage supporting the central nervous system of salmonid fishes. Hatchery-reared rainbow and brook trout seem most susceptible to "whirling disease," the result of heavy infections. Infected fish can be spotted quickly because their tail region turns black; neurological control of chromatophores* becomes impaired.

Several histozoic species infect muscle, gill, liver, skin, cartilage, and other tissue in Gulf fishes. One worth mentioning because it can be readily seen in commercially important fishes without a microscope forms cysts between fin rays of some seatrouts and related species. Figure 106 shows several cysts of this species (*Henneguya* sp.) in a spot. As with most species, millions of spores fill each cyst. In members of this genus, the two joined spore-valves have long posterior extensions (tails) (see insert of *Henneguya* sp. in Figure 106).

Coelozoic or cavity forms comprise a larger group of parasites, but fish must be dissected in order to detect them. Some large, flat, elliptical forms (trophozoites) can be seen through a gall bladder's wall, whereas smears of bile or other fluid must be microscopically examined to detect others. Gall

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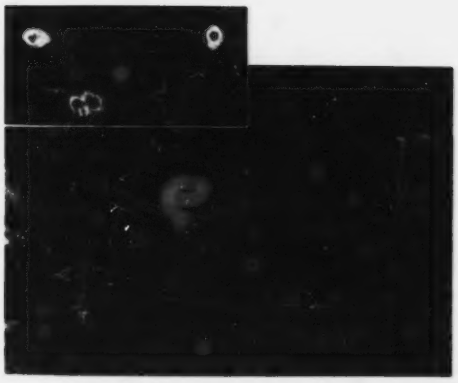
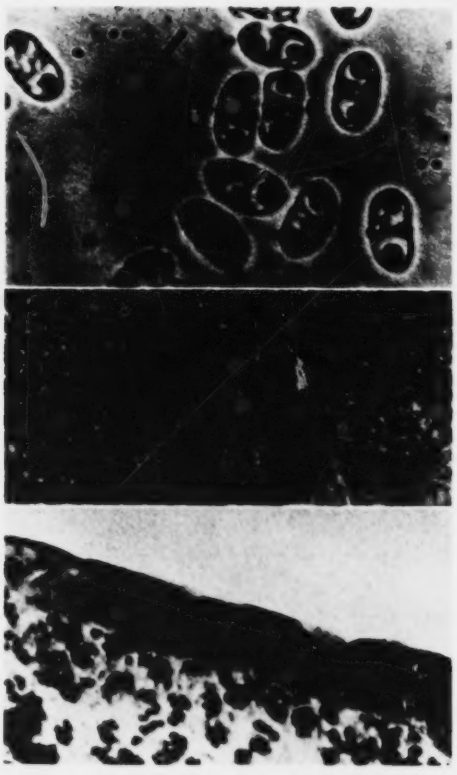


Figure 106. Spot with myxosporidan (*Henneguya* sp.) cysts between rays in dorsal and caudal fins. An insert shows the tail-like extensions of the two valves.

bladders, urinary bladders, and ureters comprise common sites.

Myxosporidans generally parasitize cold-blooded vertebrates. As one of three exceptions to this, a species (*Fabespora vermicola*) infects a fluke that inhabits the intestine of the sheepshead (a porgy) (Figures 107 to 109). Vegetative growth stages surround both primary and secondary reproductive organs, leaving the fluke unable to produce eggs. Spores develop in pairs (Figure 108); as they mature, they occupy the tegument (skin) (Figure 109). Most unusual for any myxosporidan, however, is that after the spores either actively penetrate through the tegument or passively slough with external tegument, single spores move by themselves. Possibly this unique characteristic allows other flukes to acquire infections because usually either several worms or no worms per host have infections. Neither sheepshead with the fluke nor others examined had any myxosporidan infections. Still, the most similar described relative to this parasite infects a fish in Russia.



Figures 107-109. The only reported myxosporidan (*Fabespora vermicola*) from a flatworm and one of three from an invertebrate. Top, spores showing polar capsules at opposite ends of the spore. Middle, two spores develop together within a membrane. Bottom, developing stages occur primarily around reproductive organs of the digenean host, and mature spores pass through the tegument (darkly-stained outer layer of tissue).

Ciliates

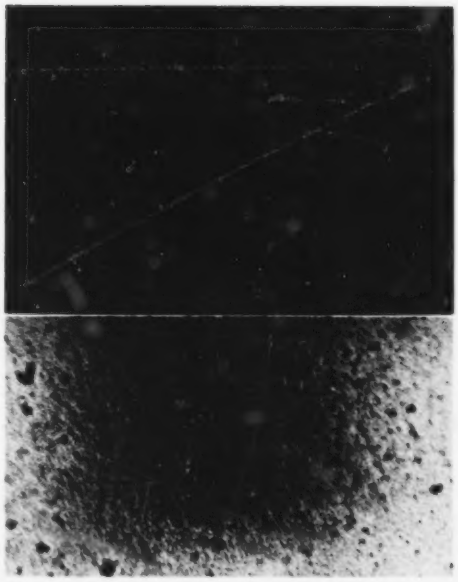
The ciliates comprise another large important group of Protozoa that infests fishes. Many commensal species become parasitic when environmental or host conditions dictate. Ciliates possess cilia in one or more stages of their life cycle. A cilium, like a flagellum, is an elongated structure usually composed of nine peripheral and two central filaments enclosed in a sheath and elaborately connected both to the body-proper of the animal and to the internal bases of other cilia in their row. The well-coordinated and controlled system allows progressive beats to form waves that aid locomotion and food gathering. Ciliates also possess two types of nuclei: a small one (micronucleus) important in sexual reproduction and a large one (macronucleus) produced from the small one and involved with nonsexual functions; the macronucleus of some ciliates appears like a horseshoe excessively twisted by an overenthusiastic blacksmith.

Ciliates are often classified according to

their feeding apparatus. Peritrichs have a long tubular buccal cavity lined with spiralling cilia leading toward the mouth, as well as some stouter cilia in rows encircling the top of the cavity. Many peritrichs attach permanently to their host or other substratum by a stalk, disk, or lorica (discussed earlier with crustacean ciliates), whereas other motile ones may attach only temporarily. All living peritrichs provide impressive spectacles under a microscope.

Most coastal fishes in Mississippi harbor at least one motile species of peritrich (members of *Trichodina* or a related genus). The ciliates occur primarily on the gills, but also infest the skin. In contrast, most of those that infest freshwater fishes, and there are many, preferentially infest the skin. Normally few individuals infest a fish, but some fishes typically host both more individuals and more species than others. The Florida pompano and striped mullet each commonly host at least two species. Juvenile pompano placed in a garbage can filled with aerated seawater and examined daily for gill and skin protozoans will acquire increasingly dense populations of trichodinids. Apparently reproducing extensively when their hosts become crowded and stressed, they may be undergoing a "normal survival procedure" in order to assure a few individuals an opportunity to infest additional hosts should theirs die.

Trichodinids may attract curiosity because of the ring of interlocking teeth (denticles) on the ventral surface. Figures 110 and 111 show these denticles for two different species. One photograph displays a live ciliate and the other shows a preserved one stained to accentuate the denticles. Devastating as these denticles might appear, they do not harm the host; they support the disk like a flexible skeleton. Ciliary movements permit an individual to glide over or hover close to its host. On the other hand, the peripheral border of the basal disk membrane can pinch and even dislodge host tissue. In this manner, the ciliate can harm its host, especially if the fish is young or has dense populations on its gills. Pathological conditions usually involve hosts in rearing facilities. Many estuarine and marine ciliates have not been named, possibly because of the detailed study necessary to delineate the patterns of cilia for the different stages.



Figures 110 and 111. Trichodinid ciliate parasites from estuarine fishes. Top, live specimen. Bottom, stained (impregnation with silver nitrate) specimen of another species to accentuate the ring of "teeth" (denticles) on the ventral surface. These ciliates can cause mortalities in reared fish.

Attached peritrichs have also been implicated in fish mortalities. One species (*Epistylis* sp.) has, within the last few years, infested an increasingly large number of bluegill, bream, bass, and marine fishes that invade fresh or nearly freshwater coastal Mississippi bayous. The disease derives its name, "red sore," from the bloody lesions associated with this long-stalked, colonial ciliate.

Red sore disease portrays a good example of both a disease associated with pollution and a disease resulting from interactions between two organisms. Fish with extensive red sores have a systemic* bacterial infection *(Aeromonas hydrophila)* that can kill the host. I believe the ciliate which is invading host tissue acts as the primary invader, allowing secondary entrance by the bacterium into the blood where it can proliferate extensively. The bacterium can also enter by other routes, even in fish without the ciliate.

Some pollutants seem to enhance reproductive capabilities of *Epistylis* sp. Hundreds of colonies of this organism produce a fuzzy growth which appears like cotton or fungi. Fish farmers find that an increase in organic materials in their ponds promotes an increase in red sores. In some low salinity and freshwater bayous that have, over the past few years, increased their concentration of pollutants or decreased their flow of water, the prevalence of red sore disease has increased dramatically. In fact, fishing in poorly-flushed regions can, during certain seasons, produce a preponderance of bluegill with red sores. Such catches have kept some fishermen from returning to particular favorite holes where they have fished for decades. Infections have kept some from fishing at all.

Holotrichous ciliates do not form a natural (phylogenetically• related) group; most have simple uniform body cilia and no specialized cilia around the mouth. The best known marine "holotrich," at least to aquarists, is the marine counterpart (*Cryptocaryon irritans*) of the freshwater species that causes "ich," a shortened term used by tropical fish fanciers to designate *Ichthyophthirius multifiliis*. Both the saltwater and freshwater species cause elevations on the gills and skin consisting of nests of these ciliates eating away at tissues just under the outer layer of skin. They irritate the host and promote secondary bacterial infections. As in the life cycle of the dinoflagellate *Amyloodinium ocellatum*, the release of one feeding individual ultimately gives rise to numerous infective organisms, each adding to disorder in an aquarium or pond. Most aquarium-remedies affect the short-lived swarming stage; therefore, treatment should continue until all feeding individuals (trophonts) leave the fish.

Cryptocaryon irritans affects a variety of hosts, but is rare in nature. Most other holotrichs do not share its parasitic mode of life; however, under appropriate conditions, some free-living species invade fish and cause damage. Reported cases have involved freshwater species primarily, but confined marine hosts possess the same vulnerability.

Free-living ciliates in other groups can also turn parasitic. A hypotrich (a species of *Euplotes* or closely-related genus) damaged gills and skin of several specimens of the sheepshead minnow collected from Horn Island and maintained for a month in an aquarium. The opercula and snout of infested fish developed bloody lesions, their normal swimming behavior modified into jerky and gasping motions, and they died, either from secondary infections or directly from the ciliate.

Tapeworms

Tapeworms (cestodes) form a group of worms which exhibits two striking features. The worms have no alimentary canal, and they have an elongated "segmented" body, thereby giving an impression of a measuring tape, hence their common name "tapeworm." As adults they inhabit tubular regions like an intestine with its high nutritional level, attaching to their host with a holdfast organ (scolex). This organ may be simple or ornamented with a variety of hooks, suckers, and other structures, and it represents the major feature used for classification. Each segment of the "tape" usually possesses one set of reproductive organs (a proglottid), and in most species a few segments are continuously being formed.

In general, few marine bony fishes (teleosts) in the northern Gulf host adult tapeworms. Examples are a worm (*Anantrum tortum*) from the inshore lizardfish and those (ptychobothriids) from needlefishes and related species. The

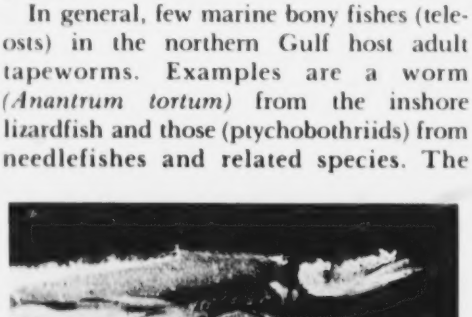


Figure 112. An inshore lizardfish portraying its viscera and the adult tapeworms (*Anantrum tortum*) from the intestine of a similar-sized fish. Worms also occur in illustrated fish.

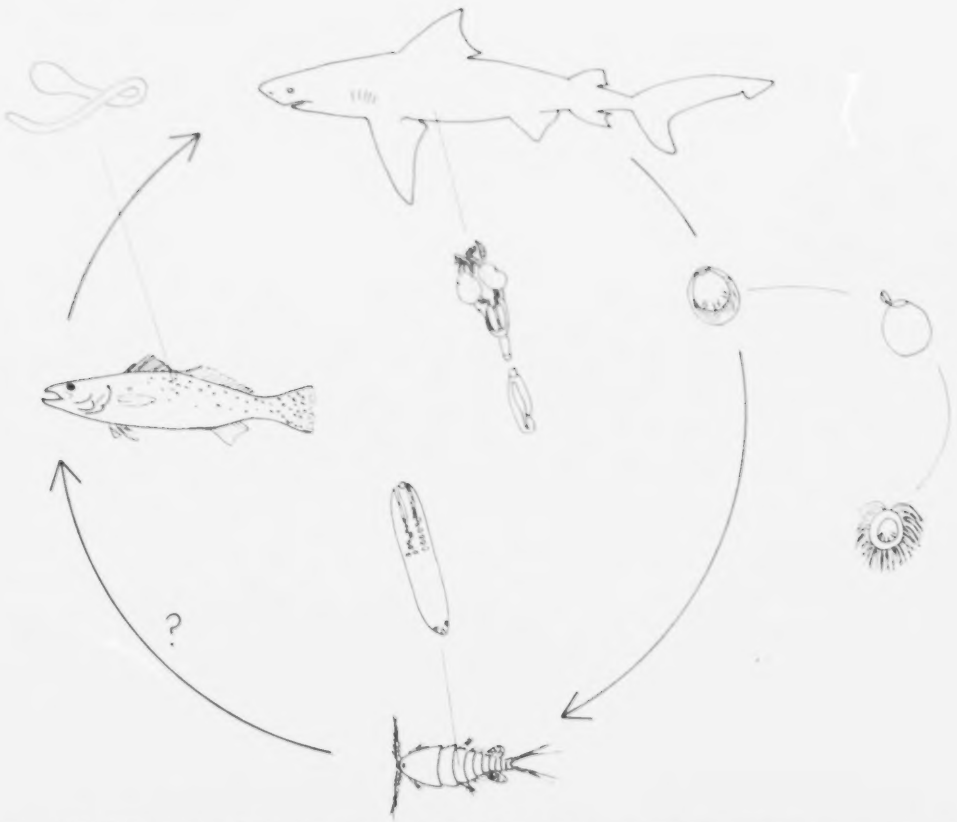
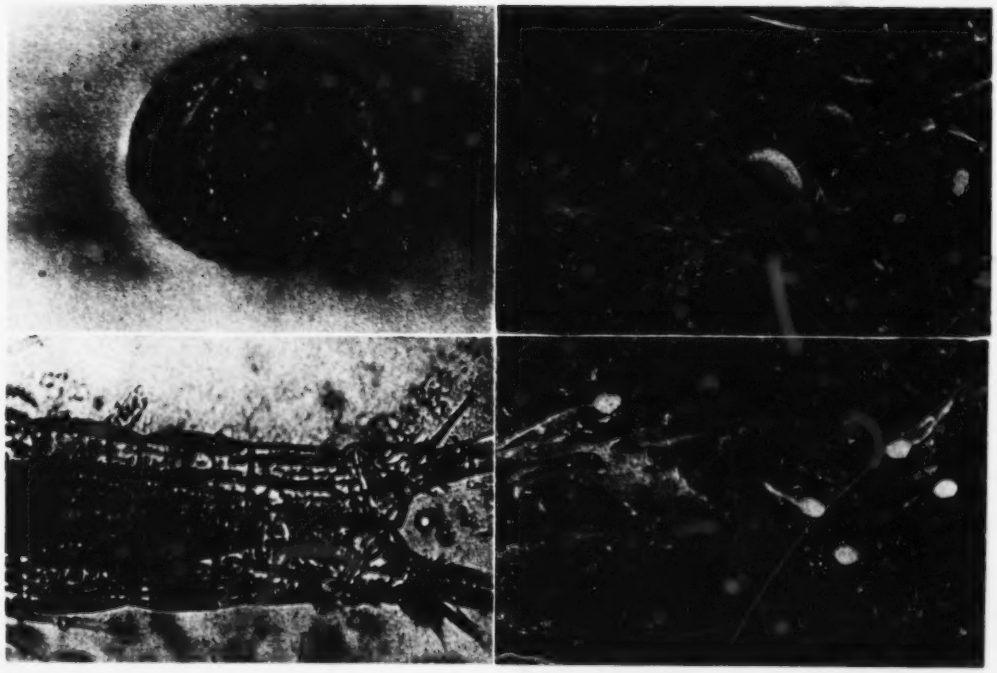


Figure 113. Life cycle of the tapeworm *(Poecilancistrium caryophyllum)* that causes "wormy trout." The adult develops in the bull shark (or other related sharks). Released segments from the adult disperse eggs, each with a larva that infects a crustacean which in turn is eaten by a fish. When eaten by seatrout and related fishes, the larva develops further in flesh and becomes infective for sharks.

lizardfish worm looks more like a twisted Christmas ribbon than a measuring tape. The normally twisted body possesses a series of reproductive organs, but they are not compartmentalized into segments. Without any specialized holdfast organ, this worm (Figure 112) often maintains its position by winding in clumps of several individuals at bends in the intestine or by sticking an expanded or folded-over "scolex" into a pyloric caecum. The position in the gut appears related to external water temperature. As the temperature increases, an increased percentage of worms locates near the anus. If a fresh lizardfish comes into possession, see whether a relatively large creamy-colored worm occupies the intestine. Watch it writhe in a corkscrew fashion within a mixture of one or more parts full strength seawater and three parts freshwater (the one-fourth seawater solution approximates the host's body fluids and will maintain most helminths for several hours).

Even though marine teleosts have few adult cestodes, they harbor a rich variety of larval ones. They act as intermediate hosts for the stage (plerocercoid) that infects the final host. With a few exceptions, these larvae mature in specific elasmobranchs. The perfect example of this causes "wormy trout." Indeed, when coastal residents, especially those who catch and fillet marine and estuarine fishes, are asked if they know about any parasites in fishes, most respond first and some respond exclusively about this trout-worm *(Poecilancistrium caryophyllum)*. To regress a bit, fish harbor many parasites, but even the most pathogenic is rendered harmless by cooking. The common one in the trout does not even need



Figures 114-117. Larval stages of tapeworm *(Poecilancistrium caryophyllum)* that causes "wormy trout." Top left, egg with enclosed coracidium showing cilia and hooklets. Top right, early development (procercoid) in copepod *(Tigriopus californicus)*. Bottom left, a more-developed larval stage. Note two individuals are present. Bottom right, subsequent larval stage (plerocercoid in blastocyst) in flesh of spotted seatrout. These organisms have been lifted some from the flesh to make them more obvious, but most fillets will have 80% of the worms obvious. Usually about two worms infect a fish, but cutting the caudal extension of a cyst gives the impression of many worms being present.

heating to become harmless to people. Unfortunately, too many people feel disgust at these infections.

"Wormy trout" refers to the presence of the entwined fleshy stage (blastocyst) that harbors an encased infective larva (plerocercoid) at its swollen end. As seen in the diagram (Figure 113), sharks (the bull shark and related species) acquire infections by eating seatrout (or less often a few other related fishes including redfish, croaker, and drum). Within the intestine and spiral valve, the worm matures, reaching about 20 cm long and producing eggs in attached proglottids. When the worm or a batch of segments passes into seawater, a ventral cleft in a segment splits, allowing eggs (Figure 114) to disperse. After about a week, a tiny swimming larva (coracidium) pops out of the capped egg. If eaten within 2 days by an appropriate crustacean, another larval stage (procercoid) develops (Figures 115 and 116). This host in turn must be eaten by an appropriate fish, usually a seatrout (see Figures 117 and 118). The worm apparently can live in the trout for a few years. Most infected sharks measure longer than 135 cm (4½ feet) long, presumably because larger sharks eat more seatrout.

Even though some fishermen think their catch had 20 or so worms per fish, few individual fish have more than 3 or 4. The elongated, twisted, fleshy extension may be cut into several pieces, giving the illusion of many worms. Apparently, once a fish becomes infected, it acquires resistance* to future infections. Examination of a large number of spotted seatrout suggests that the worms do not harm adult fish. However, no fish less than 14 cm and few less than 25 cm long had infections, suggesting either that young fish do not get infected or that the fish get killed. Larvae in small fish occasionally encroach on vital organs, giving some sup-

Figure 118. Plerocercoid of *Poecilancistrium caryophyllum* removed from fleshy blastocyst. Note the four hooked tentacles and the sheaths that contain the tentacles when they are not protruded. Constriction of the bulbs at the posterior of the attachment organ (scolex) protrudes them.

port to the latter possibility. Perhaps the worm is detrimental to good fishing. It is not detrimental to good eating!

Another "fish tale" needs rectifying. Wormy trout occur year around because once a host becomes infected, the worms can remain for a few years. When average salinity levels are high, usually during summer, the percentage of fish infected is also high. However, the percentage of infected fish during other seasons may far surpass that percentage encountered during a summer for which the average salinity was low. More spotted seatrout have heavier infections in the clean high saline water of Apalachee Bay, Florida, (an average of 4.4 worms in 98% of fish over 25 cm and a maximum of 16 worms in a fish) than in any other region sampled. High saline water probably supports more potential intermediate hosts. An average of two worms infects about 40% of the eating-sized fish in Texas, Louisiana, and Mississippi. In polluted Tampa Bay, Florida, only 1.3 worms per fish infected 10% of the trout.

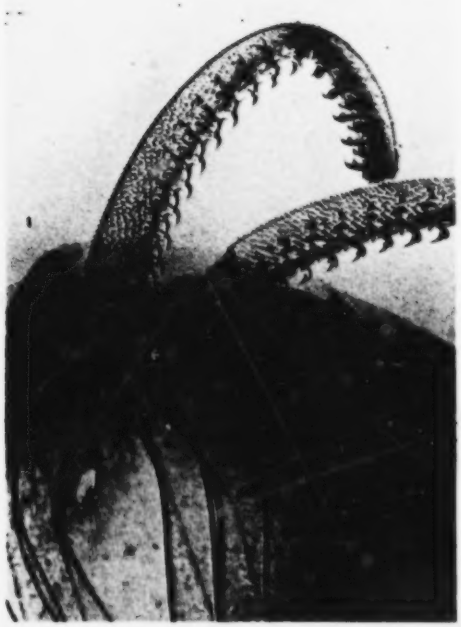


Figure 119. Close-up of tentacles of *Poecilancistrium caryophyllum* from "wormy seatrout." Note the different shapes and sizes of hooks, the muscle in the sheath that retracts the tentacle, and the darkened ciliated pits at the anterior margin. The sensory pits protruded and actively moved about when the fixed worm was alive.

The above cestode plerocercoid belongs to the trypanorhynch group and is diagnosed primarily by the presence of four eversible hooked tentacles (proboscises) (Figure 119). Contraction of muscles around the fluid-filled proboscis bulb protrudes the tentacle (Figure 118). The hooks then allow these tentacles to attach in the host gut. Another related trypanorhynch *(Dasyrhynchus* sp.) in the crevalle jack (Figure 120) can be observed commonly infecting the head and less often occurring elsewhere in the flesh. The plerocercoid of many species infects crustaceans and an earlier example (*Prochristianella hispida,* Figures 70 and 72) represents an extremely abundant one.

Tentacle-hooks come in all sizes and shapes, sometimes with considerable variety on a single tentacle. Long spikes with small distal barbs (Figure 121) characterize a species *(Pterobothrium heteracanthum)* from the muscles and body cavity of Atlantic

croaker, and a variety of hooks (Figure 122), including a stout recurved one, occurs on another species from the kidney of a striped mullet. Hooks shaped like rose-thorns are the most common type on trypanorhynchs.

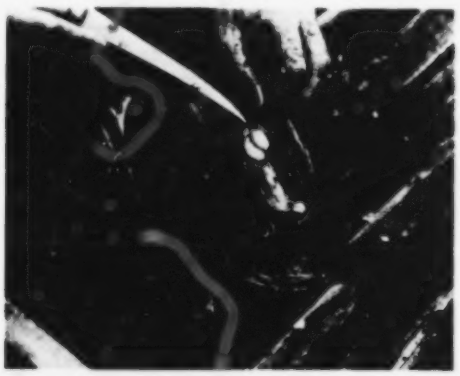
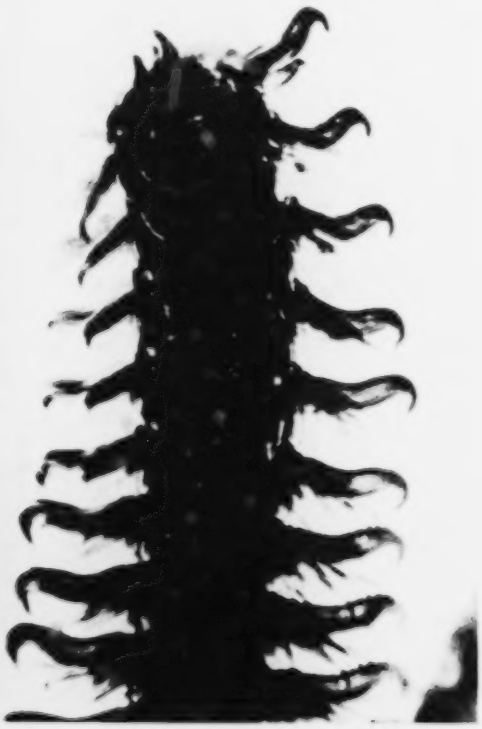
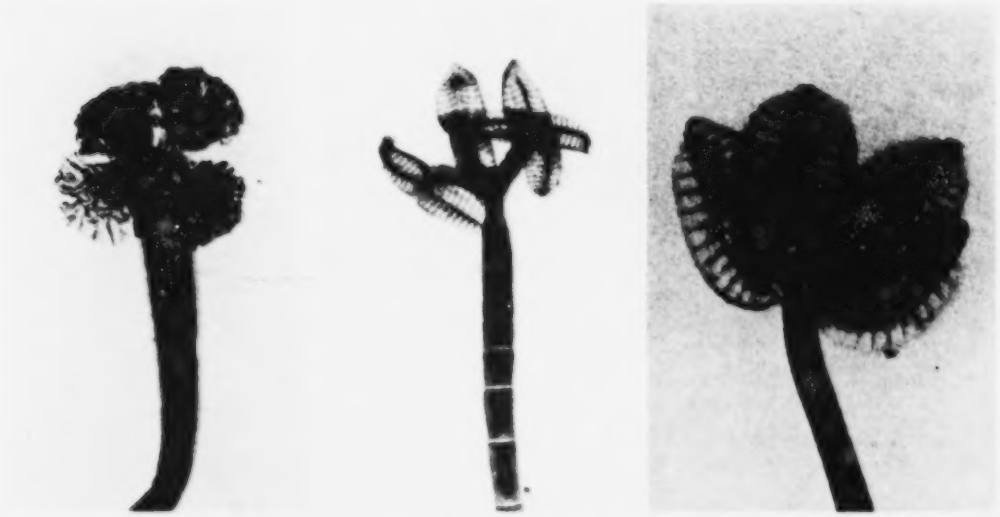


Figure 120. Individuals of a cestode larva (plerocercoid of *Dasyrhynchus* sp.) being cut out from tissue of the crevalle jack. The blastocyst has a long thin tail (caudal extension) and contains the plerocercoid.

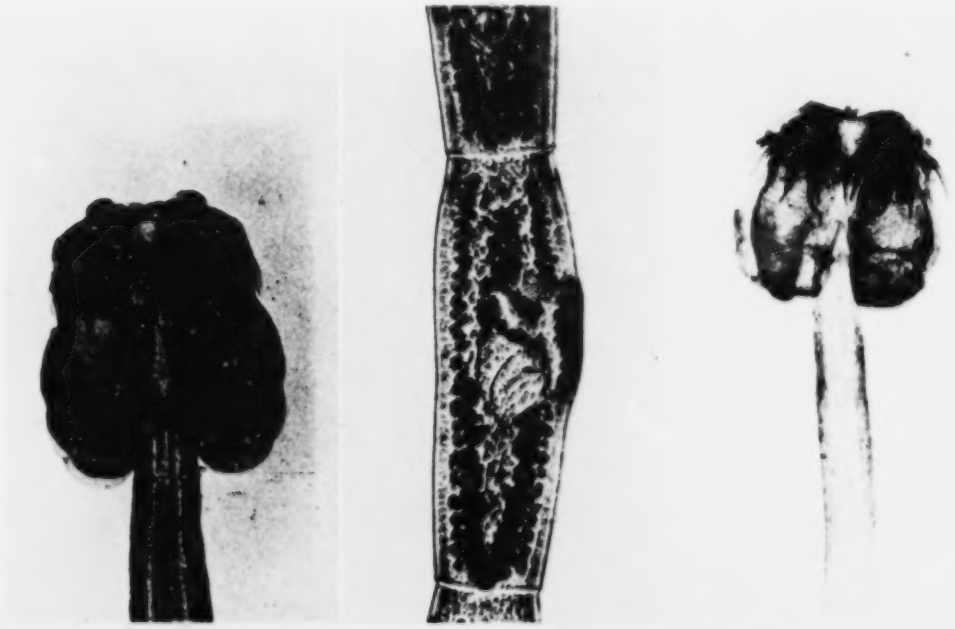
Another cestode group (Tetraphyllidea) infecting local elasmobranchs has members with four similar muscular holdfast organs without tentacles on the scolex. Each may have hooks, spines, suckers, or folds to attach to the gut. In order to appreciate the variety of these holdfasts, some photographs are presented. Note the folded margins (Figure 123) on one from the Atlantic stingray (*Phyllobothrium foliatum*). In *Rhinebothrium corymbum* (Figure 124) from the southern stingray there are 27 grooves (loculi) on each pedunculated bothridium. *Rhinebothrium maccallumi*, also from the southern stingray, has fewer (Figure 125). Members of the genus *Acanthobothrium* have triloculate bothridia, each with two forked hooks anteriorly. Compare the scolex for *Acanthobothrium paulum* (Figure 126) from the



Figures 121 and 122. Variation in types of hooks on the tentacles of trypanorhynch tapeworms. Left shows small barbs on thin spikes (*Pterobothrium heteracanthum* from flesh of Atlantic croaker). Right shows more than one type. In addition to numerous thin hooks, some robust ones shaped like a latch-hook provide the most conspicuous form (?*Callitetrarhynchus* sp. from kidney of striped mullet).



Figures 123-125. Variety in scolices of nonhooked tetraphyllideans. Left, *Phyllobothrium* sp. from spiral valve of Atlantic stingray. Middle, *Rhinebothrium corymbum* from a southern stingray has more "loculi" on each of the four bothridia than *Rhinebothrium maccallumi* (right) from the same host.



Figures 126-128. Two related species of the hooked tetraphyllidean tapeworm *Acanthobothrium*. Left, scolex (attachment organ) of *Acanthobothrium paulum* from spiral valve of southern stingray. Middle and right, mature proglottid (the reproductive segment) and scolex of *Acanthobothrium brevissime* from the bluntnose stingray. Note the divided bothridia of both species and the bend (abnormal) in the hooks of the latter species occurring in both sets of hooks. The hooks also bend on two unseen opposing bothridia.

southern stingray with that of *Acanthobothrium brevissime* (Figure 128) from the Atlantic and bluntnose stingrays. The latter does have hooks with an abnormal bend, but they are always thinner than those in the other species. A mature proglottid of *Acanthobothrium brevissime* shows the large stained internal testes, the lateral yolk glands, and the tubular genitalia (including the large male sac) leading to the margin (Figure 127). These proglottids drop off the worm and then develop eggs while still in the gut of the stingray. Detached, the enlarged proglottids of both tetraphyllideans and trypanorhynchs move about in the gut and present an appearance similar to that of a fluke. Some even develop suckers or spines.

The typical life cycle of tetraphyllideans probably follows that of the trypanorhynchs, but the underdeveloped scolex of the plerocercoid larva does not allow identification like that of trypanorhynchs. In fact, plerocercoids of many species are collectively called *"Scolex polymorphus"* (Figure 129). Possibly this plerocercoid stage for some species can be attained in a single crustacean host. Vertebrates, molluscs, and other invertebrates also act as intermediate and paratenic hosts.

Figure 129. Larval (plerocercoid) tetraphyllidean tapeworm (*Scolex polymorphus*) from intestine of small striped mullet. Larvae representing a number of different species, but similar in appearance and also called *Scolex polymorphus*, infect a variety of fishes and invertebrates.

Figure 130. An unusual tapeworm (*Cathetocephalus thatcheri*) from the spiral valve of a bull shark. Up to 14 bodies can extend from the perpendicular scolex of a single worm.

Tapeworms in general have a single long body. A few specimens of a species *(Cathetocephalus thatcheri)* from the bull shark caught from a variety of regions had up to 14 bodies (strobila) attached to one transversely elongated scolex. Possibly entirely separate worms could be formed asexually if each body detached and formed a new scolex. A single body is shown in Figure 130.

Monogenean Flukes

All groups of flukes show similarities to and are classified with tapeworms as flatworms. Even though exceptions exist, these similar features include being more or less flattened, not having a body cavity, being hermaphroditic (male and female sexual organs occurring in the same individual), and having flame cells (cells with a tuft of cilia extending into tubules) to aid in eliminating metabolic wastes and regulating water balance. Flukes can be easily distinguished from tapeworms since they possess a gut rather than depending entirely on nutrients passing through their tegument (skin). Also, larvae of flukes develop differently

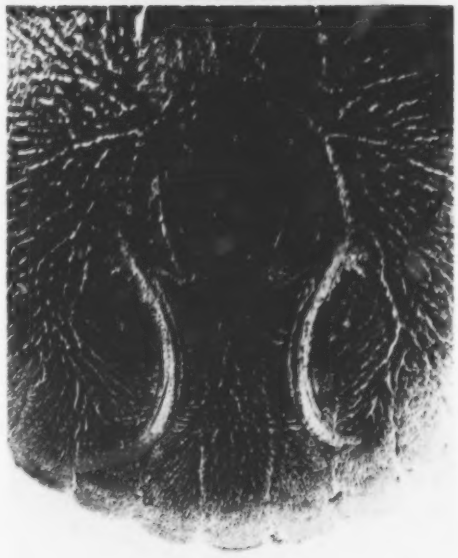
Figure 131. Sawfish with heavy infestation of monogenean (*Dermophthirius* sp.). White blobs all over head (and rest of body) are the fluke, and they are especially conspicuous because the fish had been frozen and thawed.

than those of cestodes.

Biologists separate flukes, or trematodes as they are frequently called, into those forms which typically infest their hosts externally and do not require an intermediate host from those that infect their hosts internally and undergo asexual reproduction requiring intermediate hosts. The external types (monogeneans) seem to be more closely related to tapeworms than to internal ones (digeneans).

Monogeneans primarily infest the gills or skin of fishes; however, a few occur in the gut of fishes and others infect the urinary bladders of frogs and turtles and other sites. A few even occur on or in squid and crustaceans. They usually lay a small number of eggs each day. Within each egg, an encapsulated ciliated larva ultimately hatches and develops into an adult without undergoing asexual reproduction. Worms deposit these eggs, some of which have shells with long filaments or other tangling or anchoring devices, in such a manner that helps assure completion of the cycle. Some attach eggs to sand grains on which their benthic* hosts usually rest, and others deposit them on their schooling host's gills, gambling on ultimate contact with schoolmates just as children pass head-lice to their friends. A variety of methods aid transmission.

Some adult monogeneans are so small that a high-powered microscope must be used to identify or even see them, whereas others grow larger than a thumb-nail. The



Figures 132 and 133. A capsalid monogenean (*Benedeniella posterocolpa*) from the belly skin of a cownose ray. Top, entire stained worm. Bottom, close-up of anchors and accessory structures used for forming suction cup effect for attachment.

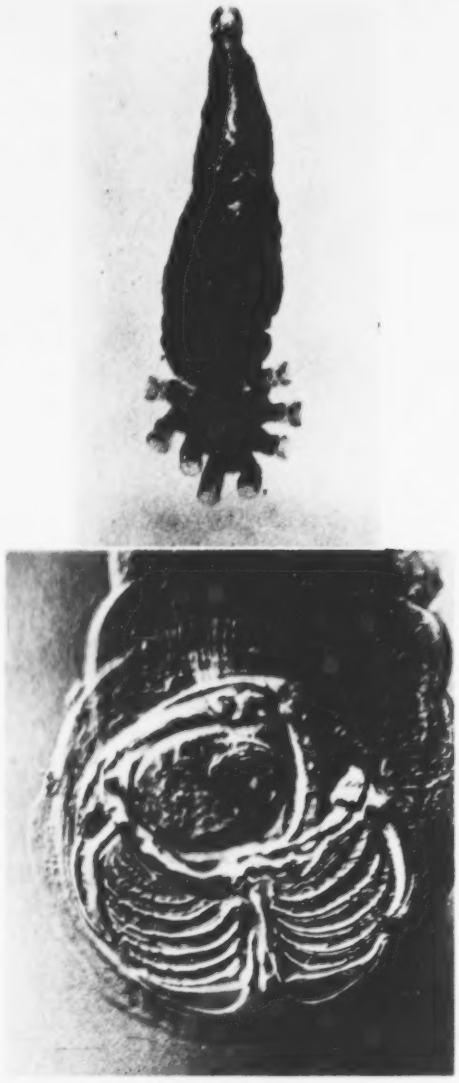
latter can be seen on the tough skin of some local sharks and other elasmobranchs. The large conspicuous objects on the sawfish in Figure 131 are specimens of a monogenean (*Dermophthirius* sp.) that were implicated in the death of the host in a public marine aquarium. The related species *(Benedeniella posterocolpa)* shown in Figure 132 came from a cownose ray. The beauty of this

common worm has been accentuated by staining. In life, the transparent milky-colored worm on the belly of the ray can be easily overlooked without critical examination. It attaches to its host using the large central anchors and small marginal hooks on the large posterior organ (haptor, Figure 133). It feeds with its anteriorly-located mouth.

Smaller monogeneans, but those still large enough to observe with naked eyes, occur commonly on gills of fishes in the Gulf. Jacks, drums, seatrouts, sharks, and many other fishes often have them. These exhibit a reddish or blackish appearance caused in part by ingested host blood or its breakdown products. As a general rule, these (polyopisthocotylids) feed on blood instead of tissue and mucus like the others (monopisthocotylids). Rather than having anchors and hooks like those monopisthocotylids discussed above from elasmobranchs, most of these polyopisthocotylids have members characterized by having clamps or suckers. Members of one family (Hexabothriidae) from sharks have large curved hooks associated with suckers (Figure 134).

At the risk of leading the reader into thinking monogeneans are not primarily parasites of fishes, an example of those with clamps also exemplifies a hyperparasite that does not always infest fish. Large specimens of this species with stalked clamps (*Choricotyle aspinachorda*, Figure 135) typically attach near the bases of the legs of a symbiotic isopod (*Cymothoa excisa*) lodged in the throat cavity (frequently on the tongue or gill rakers) of a pigfish. Often when a pigfish is not infested by the cymothoid isopod, it still has immature specimens of the monogenean on the gills. Primarily large adult flukes favor the isopod, and they deposit clumps of eggs on it. The combined worms and eggs on the isopod present a flowery appearance. The

Figure 134. Holdfast (haptor) of a monogenean (*Heteronchocotyle leucas*) from the gills of a bull shark. Note the large curved hooks (sclerites) associated with the suckers.



Figures 135 and 136. Monogeneans from symbiotic isopods on fish. Top, entire worm (*Choricotyle aspinachorda*) from isopod (*Cymothoa excisa*) in throat of pigfish. Note posterior holdfast organ with eight pedunculated clamps. Bottom, close-up of a clamp from a related worm (*Choricotyle louisianensis*) on isopod in southern kingfish.

close-up of a clamp (Figure 136) actually belongs to a closely related worm (*Choricotyle louisianensis*) which has a similar relationship with a cymothoid isopod on the southern kingfish (also commonly called ground mullet). Next time one of these fiesty bottom feeders is caught, a reader should look for the isopod and its symbionts.

Relatives of the isopod monogeneans that infest gills of fish occasionally cause mortalities, but usually only when infesting confined fish. Fishes such as the commercially valuable Florida pompano acquire infestations heavy enough to succumb. Most relatives of the first mentioned type (monopisthocotylids) on bony fish, and there are many, never reach a size visible to the naked eye. These tiny tissue-feeding species comprise a much bigger threat than polyopisthocotylids to confined hosts, including freshwater fishes. If present in an aquarium or small pond, however, infestations can usually be controlled with a variety of chemical treatments. Figure 137 shows a couple of individuals in conjunction with a parasitic dinoflagellate stressing their ailing host.

In a manner similar to that of the monogeneans on the isopod from the fish throat, another species (*Udonella caligorum*) often associates with copepods (usually species of *Caligus*) on which it attaches its eggs by filaments (Figure 138). Unusual because it lacks hooks or anchors, this monogenean can be commonly

Figure 137. Two small monogenean flukes moving about near the attached parasitic dinoflagellate (*Amyloodinium ocellatum*) on the gills of a sheepshead. Either of these two parasites could kill a captive fish if enough individuals occur at one time.

Figure 138. Filamented eggs from a monogenean fluke (*Udonella caligorum*) on a copepod (*Caligus praetextus*) on the sea catfish. The segmented appearing structure at the lower right is the copepod's egg sac.

observed on caligids from the gills and skin of local sea catfish (hardhead catfish), seatrout, and striped mullet (popeye mullet). Apparently cosmopolitan, it infects a wide range of hosts.

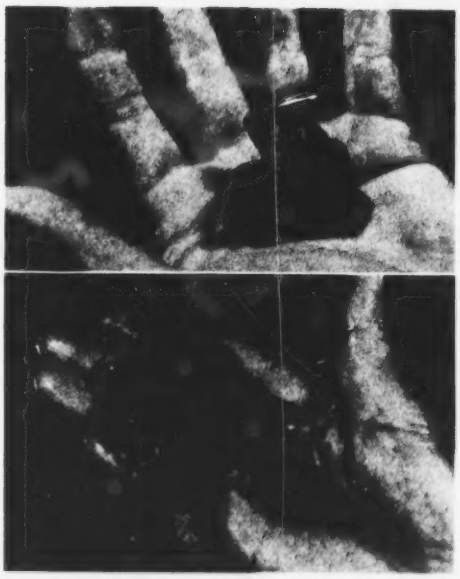
Monogeneans make good biological indicators (tags) because a single monogenean species usually limits its infestations to a single host species (see host-specificity in glossary). Many fish can be identified on the basis of their parasites! Evolutionary relationships among fishes can also be suggested on the basis of these parasites. Even though not accepted by all ichthyologists, diskfishes (remoras and shark suckers which have their spinous dorsal fin modified into a laminated disk-mechanism allowing attachment of the fish to turtles, sharks, rays, and large fish) seem to be closely related to the cobia (also called lemonfish, ling, and a variety of other names). As parasitic evidence for this relationship, species of one family of monogeneans (Dionchidae) infest exclusively the cobia and diskfishes. Since dionchids infest no

other noncaptive hosts and since members of the two fish families host no other monogeneans, a long period of isolation is suggested. Several other groups of monogeneans infest primarily members of certain families, indicating strong evolutionary trends.

Digenean Flukes

Digenean flukes exhibit considerably more variety in their adaptations than monogeneans and quite possibly more than any other helminth group. Many different groups of animals serve as intermediate hosts for the larvae. In addition to fishes, adult digeneans infect amphibians, reptiles, birds, mammals, and occasionally crustaceans and molluscs. In fishes, most species infect the alimentary tract, but a few encyst in flesh, lodge in blood vessels, or occupy other sites. More species in birds and mammals than in fishes occupy spaces other than the alimentary tract. Some of these are the kidneys, air spaces, and the bile ducts.

Almost all digeneans utilize a snail or bivalve mollusc as a first intermediate host. An earlier diagram (Figure 28) already portrayed a complete cycle of a snail to crab to raccoon pattern, and more cycles will be discussed in this section. In general, asexual reproduction takes place in the mollusc. This reproduction involves a few different kinds of larvae. The larva from the egg infects the mollusc and produces a stage that either yields additional individuals of the identical type which then produce free-living* larvae (cercariae) or another stage which also produces the same kind of free-living larvae. The route of infection and kind of larvae depend on the species considered. Cercariae of some species crawl or encyst in the host mollusc without leaving it. Most, however, have long tails allowing them to swim or to attract predators. Some penetrate their hosts, some encyst externally, and some are ingested directly. Often, the time of day, amount of light, temperature, tidal phase, or water pressure controls release of these larvae. Once in or on their proper host (or vegetation or some other object), the tail, if present, sheds and the minute larva (metacercaria) forms a capsular cyst, with or without more cyst



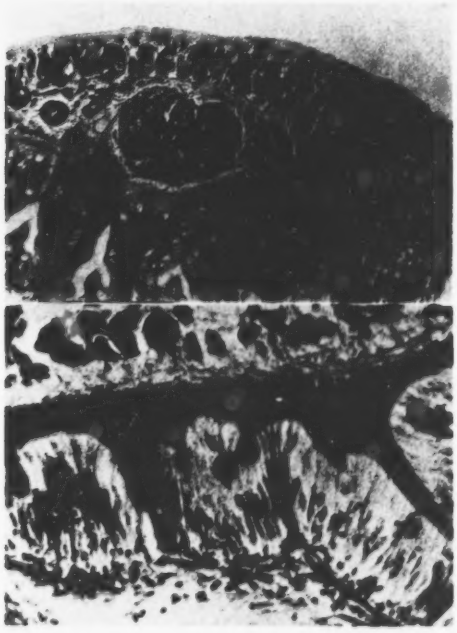
Figures 139 and 140. The giant stomach worm (*Hirudinella ventricosa*) from "blue-water" fishes. Top, contracted, preserved specimens from wahoo. Bottom, more elongated preserved specimens from little tunny; living worms can extend further than an opened hand. Note the two suckers. The dark color represents breakdown products of blood obtained from feeding on the host's stomach.

layers added by the host. The metacercaria of a few species develops without cysts (unencysted metacercaria), but examples of this type represent exceptions. After developing for an adequate period, the larva can infect its final host. Occasionally, it can debilitate or alter its intermediate host in such a manner that the final host has easier access to individuals that are infected: some infected amphipods turn reddish or pale, making them more visible to final hosts, some snails do not burrow as deeply as uninfected ones, and some fish cannot swim as fast or as long as those without cysts. Those species without special means to alter the intermediate host's behavior may have to produce many more larvae in order to assure that enough larvae will mature to complete the cycle.

One trematode that fishermen who fish for billfish and other pelagic fish should be aware of is the giant stomach worm *(Hirudinella ventricosa).* Fishermen may know it because of its large size. Figure 139

shows some preserved contracted ones ("walnut worms") from the stomach of a wahoo, whereas those in Figure 140 from little tunny ("bonita") exhibit less contraction. When alive, the fluke can elongate much farther than shown. What appears to be the same or at least similar species infects a variety of "bluewater" fishes. When in the wahoo, usually only two individuals are present. This common occurrence of two worms in fish shorter than 160 cm has allowed many a wagering fisherman to win a six-pack of beer. One should use caution, however, because tunas and other fishes do not usually possess two per fish.

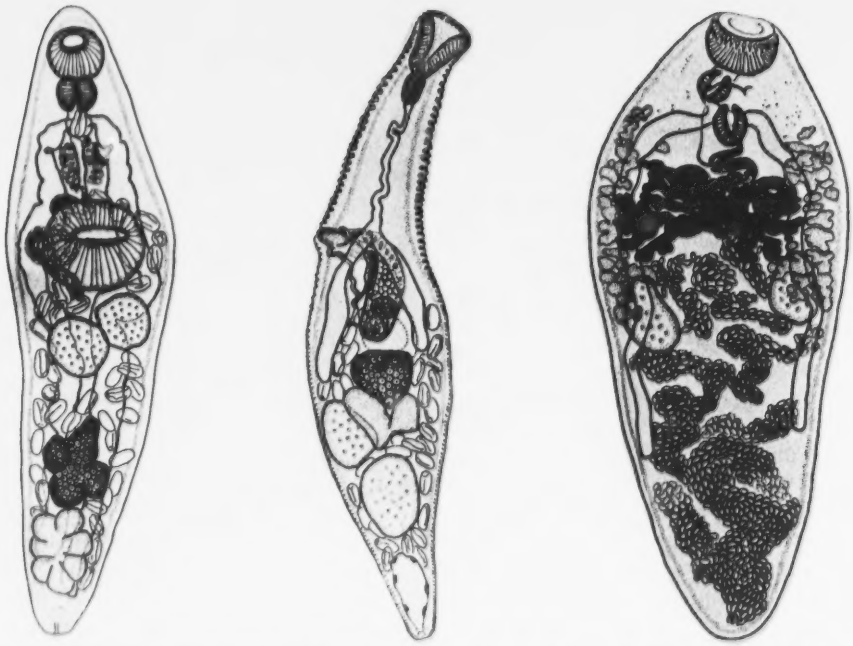
Most flukes have two suckers. A central one primarily holds on, whereas an anterior one operates in feeding, holding, and moving. These suckers can be seen in the photos and in most of the digenean illustrations in this guide. In addition to the suckers, one species *(Crassicutis archosargi)* from a sheepshead can modify its tegument into an adhesive surface (Figures 141 and 142).



Figures 141 and 142. A sectioned digenean (*Crassicutis archosargi*) expressing its ability to modify its tegument adjacent to the host's (sheepshead) intestinal tissue so that it expands, fills all available space, and adheres firmly. Top, cross-section through level of the fluke's testis. Bottom, especially stained (periodic acid Schiff with diastase) worm-tegument showing positive reaction. Most digeneans attach to their host by their ventral sucker.

The line drawings of three species (Figures 143 to 145) portray examples of several features. The one on the left *(Lecithaster leiostomi)* comes from the intestine of spot and a few other fishes. Unlike the related *Hirudinella ventricosa* from billfish stomachs, it does not need a thick skin (tegument) for protection from stomach acid and from churning food particles. Also, *Lecithaster leiostomi* seldom reaches 1 mm in length. Most members of its family (Hemiuridae) inhabit the stomach's lumen, but other exceptions exist. In fact, another small species *(Saturnius maurepasi)* even dwells in the tissue under the lining of the striped mullet's "gizzard" (pyloric stomach). The middle worm *(Glaucivermis spinosus)* is a little shorter and has a thinner tegument than *Lecithaster leiostomi*, but also infects the intestine (of the southern kingfish). The worm on the right *(Neochasmus sogandaresi)* is about twice the size and infects the striped bass. It has several relatives that infect a wide range of freshwater and marine fishes. One relative without the spines about the mouth *(Metadena spectanda)* ranks among the most common, but seldom seen, animals in the estuaries. For example, during February of 1971 an average of 54.3 individuals infected each of 53% of the Atlantic croaker examined near Ocean Springs that had the worm (90% of the fish larger than 7 cm were infected). Because croaker during that period comprised the most common fish besides the bay anchovy and many specimens of the fluke infected most of them, that fluke should be recognized as a common constitutent of the animal community. In fact, other fishes also host the worm! During the past couple of years, however, the population density of both the croaker and digenean have decreased.

The three illustrated digeneans represent different families, but all have small eggs (about 30 μ, or 0.030 mm, long). Several other digenean groups have members with eggs several times larger. As a general rule, large eggs produce larvae (miracidia) that



Figures 143-145. Line drawings of three digeneans from fishes. Left, a hemiurid *(Lecithaster lelostomi)* from a spot. Middle, a zoogonid *(Glaucivermis spinosus)* from a southern kingfish. Right, a cryptogonimid *(Neochasmus sogandaresi)* from a striped bass. These do not begin to exhibit the variety in characteristics of digeneans. Note the ventral suckers, the lobation of the ovary (dark organ), lobation and follicles of yolk gland (lightly stippled organ), and male terminal organ (exists marginally in center worm).

leave the egg to search out and penetrate the mollusc, whereas small eggs usually have to be ingested by a mollusc in order for the enclosed larva to parasitize the mollusc and complete the cycle. Consequently, many more small eggs have to be produced to result in final populations equivalent to those producing large eggs. The normal golden-tanned eggs give color to many otherwise chalky or transparent live worms. Other species, however, acquire carotenoids or other pigments, giving their bodies yellowish, pinkish, or orange colors.

Most fishes harbor digeneans and some have several different species. Even though many show specificity toward a single or few hosts, they, as a group, exhibit less specificity than monogeneans.

In addition to harboring adult digeneans, fishes also host a variety of larval digeneans (metacercariae). Usually the small worms are encysted and cannot be seen without a critical microscopic examination (Figure 146). Exceptions occur when the host deposits dark pigment around the cysts. Fishermen know this condition as "black spot" disease, and several nonrelated

Figure 146. Dorsal fin of Atlantic croaker with encysted digenean specimens (a metacercaria) between finrays. If the croaker is eaten by the proper predator, the larval fluke will mature.

Figure 147. Black spot resulting from pigmentation (melanization) around larval cysts of a strigeoid fluke in the tidewater silverside. A variety of freshwater and marine parasites can cause black spot.

digeneans cause it. In the southern U.S., most cases of black spot result from strigeoid infections. Most strigeoid species utilize a freshwater snail and a fish-eating bird in the cycle. The tidewater silverside from the estuaries in Mississippi, however, also possesses a strigeoid species. The one in the photo (Figure 147) came from the Pascagoula estuary. One large easily visible hemiurid *(Stomachicola magnus)* encysts in the flesh and elsewhere in a variety of fish. The white (sand) seatrout often has many. If the curious finder pricks at this black object in a fresh fillet, out will pop a pinkish-colored worm.

Normally, chromatophores (Figure 148) expand, spreading out their associated melanin to give a fish a dark color. Contraction produces a pale color. Other chromatophores bear different pigments for different colors. Most diseases in which pigments are deposited, however, involve melanin.

Less easy to see than the above hemiurid, a small heterophyid *(Phagicola longus)* infects the flesh and viscera of mullets along the Gulf and southeastern Atlantic states. A diagram (Figure 149) shows the life cycle. In addition to herons, a large number of other birds and mammals, including man, can probably act as final hosts. Although no human infections have been confirmed, many people throughout the world who eat raw fish harbor zoonotic* species related to this tiny worm. Most infections produce symptoms hardly more serious than diarrhea and mild irritation, however, serious complications occasionally develop.

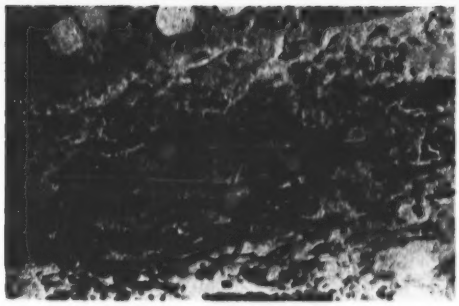


Figure 148. Melanophores in the skin of a fish. These are part of a complex system of chromatophores which regulate colors and color changes in fish. This piece of sectioned tissue had an overabundance of pigment surrounding a lesion.

Heterophyids have many similarities with the microphallids already discussed earlier as digeneans infecting the blue crab and shrimp. Small species infect birds and mammals, often in very large numbers. A sample of 14 brown pelicans from Louisiana averaged about 12,000 specimens of *Phagicola longus* per bird. Both digenean families have a large number of species, and, in both groups, the second intermediate host is usually more specific than the final one. Adult heterophyids appear very similar in appearance to microphallids, but minor differences in their genitalia and other features set them apart. Differences in their free-living larvae (cercariae) accentuate the differences even more. From a more practical point of view, heterophyids use fishes as second intermediate hosts and microphallids use crustaceans.

The key silverside shown in Figures 150 and 151 has damaged fin rays caused by an encysted metacercaria (of an acanthostome). One important fact concerning these infections is that the fish is rare and considered endangered. Found in a pond in the Florida Keys, the fish has to contend with a parasite in addition to man's encroaching developments. The final link in the cycle, either the American crocodile or the American alligator, also has status as an endangered species.

Another group of digeneans or closely related worms is the aspidogastrids. These have a conspicuous ventral loculated holdfast organ and a life history lacking asexual reproduction. Although prevalent in some

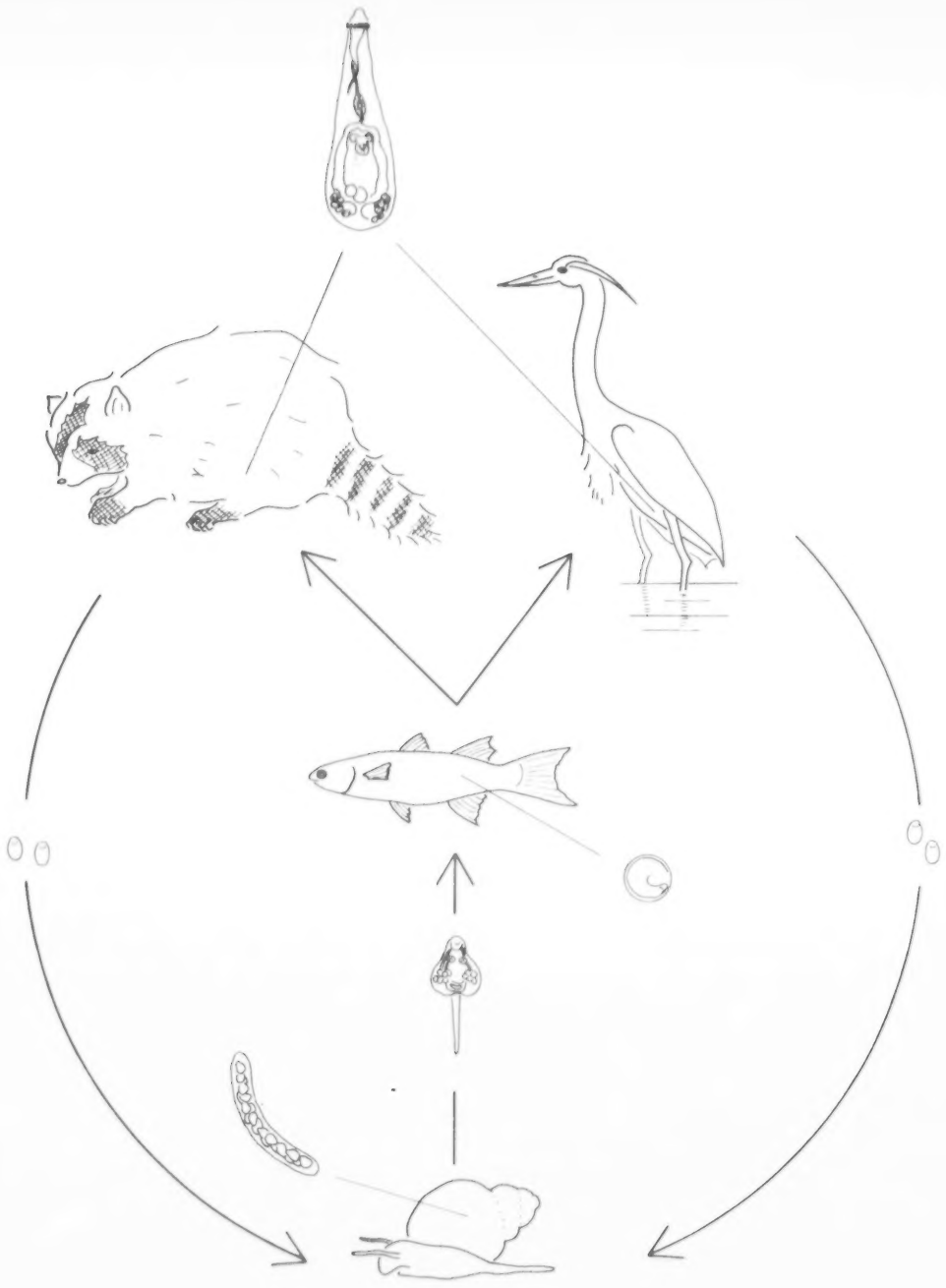


Figure 149. A heterophyid fluke *(Phagicola longus)* life cycle. This large family of flukes has adults that infect the intestine of birds and mammals and larvae that encyst in fishes. The encysted stage shown here infects predominantly mullet.

Figures 150 and 151. Two specimens of the key silverside infected with cysts of the metacercaria of an acanthostome digenean. Bottom, close-up view showing nature of damage to caudal fin rays. Cysts also occur elsewhere on these and other species of fish. A crocodilian completes the cycle for the parasite.

freshwater clams and turtles, aspidogastrids include species that also infect marine fishes. The most common Gulf species *(Lobatostoma ringens)* occurs in the intestine of a variety of fishes, but if a person really desires to obtain a specimen, he (used in the antiquated sense to include also females) will have the best chance by examining a Florida pompano. Fish apparently acquire the worm by feeding on coquina clams in the surf, but it may be harbored by other molluscs.

The most attractive aspidogastrid *(Multicalyx cristata)* resides in the bile ducts of large rays, sawfish, and other elasmobranchs. Growing over 10 cm long, the narrow pale yellow body contrasts sharply with a bright reddish holdfast organ. The elasmobranchs may acquire infections by feeding on bony fish with juvenile worms (checkered puffer, southern kingfish, and others) which in turn picked up the worms from a mollusc. A preadult specimen *(Cotylogaster basiri)* from the rectum of the sheepshead illustrates an aspidogastrid (Figure 152). An earlier study

Figure 152. A preadult aspidogastrid (*Cotylogaster basiri*) from the rectum of the sheepshead. Presumably acquired from a mollusc, this worm matures in a few fishes including the sheepshead.

showed completion of one aspidogastrid cycle utilizing a freshwater clam as the only necessary host and the ability for turtles feeding on the clam to maintain an infection; many biologists assumed that species to be representative of the group. Actually, a vertebrate appears to be necessary for maturation of most species, including *Cotylogaster basiri* and *Lobatostoma ringens*, rather than just an adjunct host helpful as a dispersing agent.

Roundworms

"Roundworm" is a common name for a nematode. Not all nematodes parasitize animals. Some infect plants and others live free without hosts in water or soil. They all have separate sexes, a digestive tract, a tough cuticle (outer layer of worm), and internal longitudinal muscles. The reason for mentioning this last feature is that nematodes, unlike earthworms, and caterpillars, move in a whiplike fashion. Most other animals that are called "worms" have a layer of circular muscles that allow a coordinated inchworm-type of locomotion.

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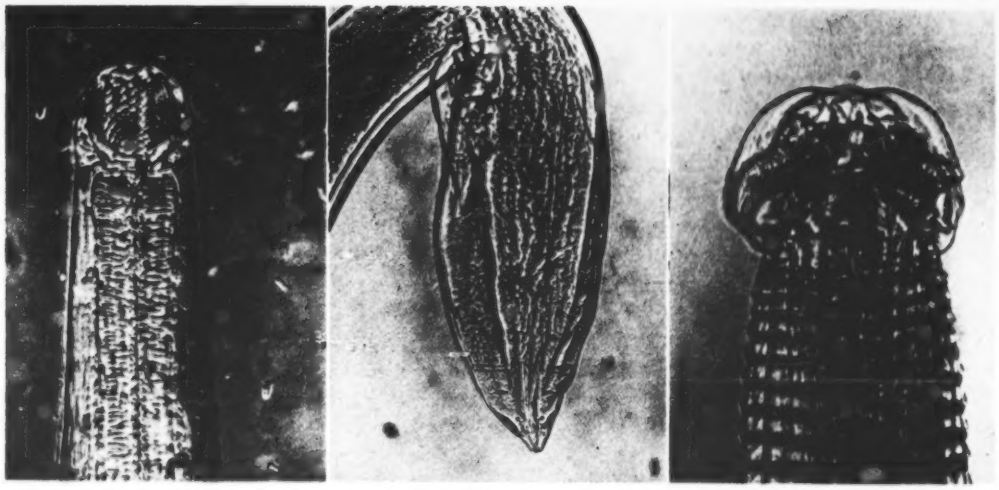


Figures 153-155. Some views of two adult roundworms from the intestine of fish. Left, anterior end of camallanid *(Spirocamallanus cricotus)* showing spirally ribbed buccal capsule used for attachment to gut. The capsule is hard and golden-tan to orangish in life and followed by a long muscular esophagus. Middle, a male tail of the same worm showing the winglike flaps (caudal alae) with sensory papillae used in grasping the female during mating. Right, anterior end of ascaridoid *(Thynnascaris inquies)* from a cobia. Attachment by this worm is achieved by the three large lips. The distinct ringed cuticle is not as dominant in related species.

The size and arrangement of the longitudinal body musculature in nematodes dictates the type of slashing movement it will have. Before reading this guide, a reader may have never thought about parasitic nematodes, even though he may have pondered "vinegar eels" *(Turbatrix aceti)* thrashing about in plant juices or vinegar. Those small free-living worms had been incorrectly credited in the past with the acetic properties of vinegar.

Parasitic nematodes occupy a wider variety of habitats than most worms in fish. The adult forms in fishes occur mostly along the alimentary tract, whereas most larval forms inhabit the mesentery. These larvae usually have thin cysts encapsulating them. One family of nematodes worth mentioning for its unusual locations is the Philometridae. Members of this group usually appear reddish. Some reside in the body cavity, and others occur in the gonads, between fin rays, under the skin, and in muscle tissue. Rather than releasing eggs like most nematodes, these worms release young larvae. Philometrids infect a variety of local fishes including the Atlantic croaker, redfish, tripletail, and southern flounder.

A few intestinal worms also deposit larvae rather than eggs. An especially notable one also has a reddish color. It was mentioned earlier as a nematode larva in penaeid shrimp. This camallanid *(Spirocamallanus cricotus,* Figures 153 and 154) infects the intestine of at least 13 different estuarine and nearshore fishes. When an intestine of a fish is swollen, filled with liquid, or partially transparent, these relatively large worms (up to 3.2 cm long) can be seen wiggling within the uncut gut. The reddish worm's activity, especially when several occur together, readily distinguishes it from any food contents.

Why is *Spirocamallanus cricotus* red? Many worms, and other animals including the beautiful flamingo acquire their reddish color from components in their diets (mostly carotenoids). Such is not the case for *Spirocamallanus cricotus* and some other reddish nematodes. Unlike most nematodes, these worms have hemoglobin* just like man and fishes. Properties of the hemoglobins from *Spirocamallanus cricotus,* however, differ some from those of its Atlantic croaker host. The worm attaches to the gut wall with its golden colored, spiralled, scleritized* buccal capsule (Figure

153) and feeds on host blood. The worm quickly digests the host blood, and a possibility exists that its components help to form the worm's own hemoglobin. Strangely though, properties of this hemoglobin in males differ from those in female worms.

Fish can acquire infections of this reddish colored nematode by feeding on copepod intermediate hosts. The penaeid shrimps also act as intermediate hosts and quite possibly as paratenic (transfer) hosts. I have seen worms in the common small squid *(Lolliguncula brevis)*, and other animals may also serve as paratenic hosts. A paratenic, or transfer, host is one in which no development to the next stage occurs, and paratenic hosts have and will be discussed again under other sections. This type host should not be confused with a reservoir host• in which any stage could occur.

Spirocamallanus cricotus takes several months to mature and can live in a fish for longer than a year. Since individuals grow relatively slowly, they probably do not cause excessive mortalities in juvenile fish. Several specimens crowded into one fish might cause disease, and related species have killed their hosts. The ripe female of one of these *(Camallanus oxycephalus)* sticks its reddish body out the anus of a striped bass or other of its hosts. These can be commonly seen in estuarine bayous and freshwater habitats of both Mississippi and Louisiana. When fully gravid, the protruded female ruptures explosively and releases her larvae. Copepods serve as the intermediate host, and small fishes serve as paratenic ones.

Different groups of nematodes attach to their host using different anterior structures. Philometrids do not develop a very elaborate anterior end because they embed in tissue. The camallanids have scleritized bivalve-shaped or barrel-shaped buccal capsules, and adult ascaridoids possess three strong lips.

Common ascaridoids from local Gulf fishes include members of the genus *Thynnascaris*. Figure 155 shows the powerful lips of a species *(Thynnascaris inquies)* from the stomach and pyloric caeca of the cobia (lemonfish). Actually, the conspicuously-ringed cuticle constitutes an atypical feature for members of that genus, but not for members of a related genus. *Thynnascaris inquies*, often present in the hundreds in a large cobia, occasionally causes ulcerated lesions at sites where several individuals attach clustered together.

Other ascaridoids occur in the northern Gulf, and one *(Thynnascaris reliquens)* is occasionally common in inshore fishes. This worm, up to 13 cm long, may also occur in the hundreds in the intestine and elsewhere along the alimentary tract of sheepshead and a few other hosts. In several other hosts, however, only few specimens occur. When a host has been caught and landed or otherwise placed under severe stress, the worms vacate the host, leaving through the mouth, gill cavities, and anus, hence the Latin name *reliquens* referring to the abandonment. Additional species in marlin and other billfish also leave in mass. Such an activity, disgusting as it may appear, should have no bearing on whether a person eats the fish. Even though some species may be harmful to man, the escaping stage is easily visible, it is an adult, the worms are discarded when removing viscera, and their eggs need several days before becoming infective and then not to people. Nevertheless, cooking the fish alleviates any potential threat. More information on public health aspects occurs below.

Something should be said about the sex life of nematodes, since reproduction accounts for most of their expended energy. The figured copulating pair shows the curled tail of the male wrapped about the female, the inserted right spicule, and a

Figure 156. A male nematode (*Thynnascaris reliquens*) mating with the female. A mucoid band girdles the female immediately posterior to her genital opening.

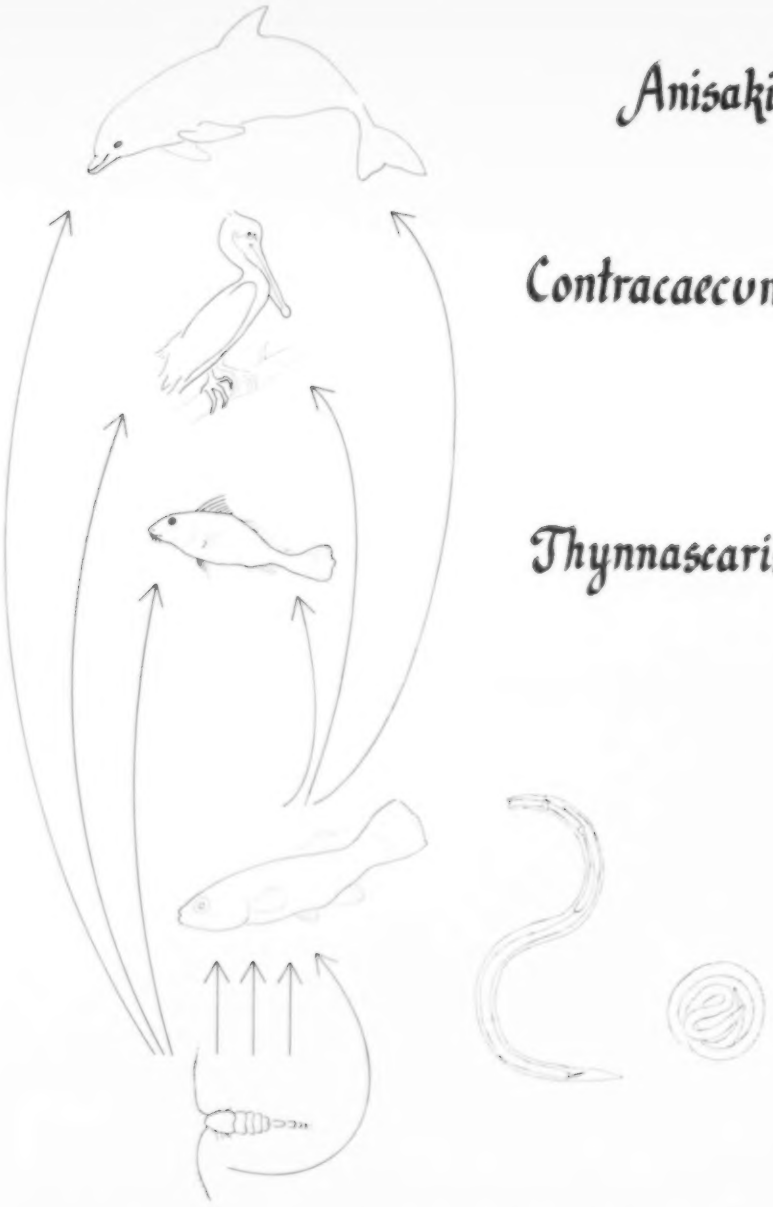


Figure 157. Generalized ascaridoid roundworm life cycle. Three different types of final hosts are illustrated, and each harbors members of a different genus. Nevertheless, the life histories of the worms show the same general patterns. Depending on the species involved, eggs deposited in the water either produce free-swimming or encased infective larvae. Copepods or other crustaceans act as primary hosts for most species, allowing development of the stage infective for the vertebrate host. Some crustaceans do not support complete development of the larva, but become eaten by a fish or other invertebrates in which development does occur. For some species, free-swimming larvae eaten directly by fish will develop to a stage infective for the final host. Usually, improper fish hosts that eat fish with infective larvae will maintain and accumulate infections. Depending on the species of parasite, the length of these larvae range from the span of a head of a pin to that of a finger. A coiled and straight specimen of a larval *Thynnascaris* sp. is figured to the right of the intermediate hosts. With minor modifications, all ascaridoid larvae appear similar.

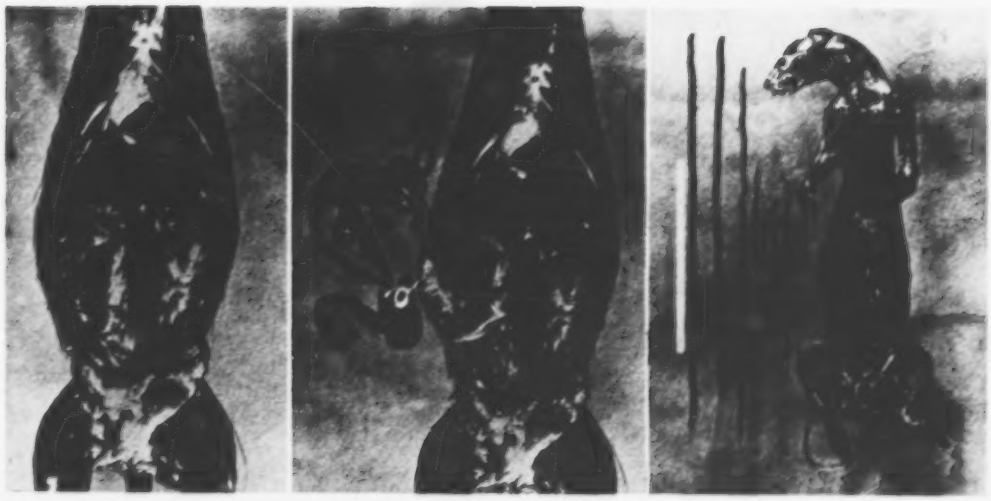
mucoid band about the female (Figure 156). The male's tail in this worm and all other nematodes has some type of a modification to cup or clasp the female. It is usually lined ventrally with a specific pattern of sensory papillae (see Figure 154 of the male tail of *Spirocamallanus cricotus*). Once properly aligned, the inserted spicule or spicules allow passage of sperm to fertilize the ova. The position of the female opening and other aspects of both the female and male reproductive systems vary considerably among different groups of worms and comprise important taxonomic characters.

While still concerned with ascaridoids and their biology, I will discuss general life cycles of species of three different genera. Mammals (porpoise), birds (pelican), and fishes (Atlantic croaker) act as hosts for members of *Anisakis*, *Contracaecum*, and *Thynnascaris*, respectively, as exemplified in Figure 157. Actually, several species exist in each of these three and related genera of parasites, and most probably have similar cycles. The major difference among the three relates to the members' infecting a mammal, a bird, or a fish, respectively, as their definitive hosts. Eggs are released with feces from the host. Usually an egg develops in a few days, and a small larva is released. If a proper crustacean feeds on the wiggling little larva, the worm develops into a stage infective for the final host. Alternatively, if an appropriate fish feeds on the free-swimming larva of some species, the worm can develop without the copepod. On the other hand, some copepods do not promote development in the worm, but still allow a fish to acquire the larva by feeding on them. Whether infective as a free larva or within a crustacean, some species can complete the cycle to maturity by utilizing a fish intermediate. Although usually not highly host-specific, an ascaridoid will not infect nor develop in all fishes. In order to assure completion of cycles, however, many fishes and invertebrates can act as paratenic hosts. As discussed earlier, they acquire infective larvae by feeding on other hosts with the same stage larva. No development takes place in the new host, but accumulation and transference assure a greater supply of infective larvae in the entire habitat. Once an intermediate or paratenic host is eaten by the proper definitive host, the worm matures in the alimentary tract and deposits eggs to start another cycle.

Larval species of *Anisakis* and other genera infective to marine mammals act as potential threats to public health and the primary cause of marine nematode zoonoses•. Even though species belonging in genera that normally infect non-mammalian hosts may infect man, they are not as large and most are harmless. At least one species of *Thynnascaris* from both fishes and invertebrates can infect laboratory mice, and it was discussed earlier as a shrimp parasite. Fortunately, few mammalian-type larvae occur in the inshore coastal regions.

Less dangerous to man, but nevertheless discomforting to fishermen, are large species of larval *Contracaecum*. These cream-colored to yellowish to reddish worms coil up or occur straight, either free or encysted in their hosts. The species in different mullets (*Contracaecum "robustum"*) most often infects their kidneys and liver. A related species in the redfish and a few other hosts infects the same sites, but also commonly resides in the mesentery. Because an individual of both species can extend over 2 cm when uncoiled and the worms heavily infect some fish, they constitute a logical cause for unnecessary worry. The tested worms have not infected experimental mammals, are usually discarded normally when cleaning fish, can be easily avoided, and are killed with heat.

Past history, including the great depression of the 1930's did much to influence the likes and dislikes of eating mullet on the Gulf Coast. Since smoked mullet was a primary protein source for many years, many people still prepare mullet in this and a variety of other ways. For this same reason, many people would be happy never to see another mullet or can of Spam. Actually, in the 1800's many inland farmers made annual fall trecks to the Florida coast to catch and salt large quantities of mullet to last through the year. Before that, Indians made similar annual trips to catch, salt, and smoke the fish. If fresh mullet is cleaned immediately, I recommend it highly.



Figures 158-160. Skinned mink with the giant kidney worm *(Dioctophyma renale)*. Left, greatly enlarged right kidney with enclosed nematodes. Middle, same kidney cut open to expose worms. One worm exhibits a post-mortem deflated condition and an extruded uterus filled with eggs. Note the bony spicules supporting the empty kidney capsule. Right, seven worms all removed from the body cavity of the single adjacent mink. Note the externally affected, but not infected, right kidney. According to the trapper, this mink was a healthy-appearing, active individual.

Herbivorous (plant eating) fish like mullet, just as their herbivorous terrestrial counterparts deer and cattle, quickly decrease in quality if not immediately eviscerated.

Larval ascaridoids, although usually not harmful to adult fish, can kill juveniles because of their relatively large size in comparison with that of the small fish's vital organs. This danger exists in the natural environment because many small fishes feed on infected copepods. Consequently, the possibility for fish fry to get infected may depend on whether copepods harbor appropriate worms at a time when and a place where fry are present.

Many other groups of nematodes use fishes as intermediate or paratenic hosts. Members of most of these are small and necessitate critical examination to find and to identify. One conspicuous exception is the dioctophymatids. These large red worms can be found taking up most of the space in a killifish's or some other small fish's body cavity.

The giant kidney worm *(Dioctophyma renale)* in mink (Figures 158 to 160) and other mammals represents a well-known member of the group because it can reach over a meter long in an appropriate host. Once ingested, a few specimens enter the host's right kidney and totally devour all the internal cellular material, often leaving only the kidney's capsular wall reinforced by some freshly-deposited bony spicules. Infections probably occur primarily in the right kidney because the placement of the duodenum and liver allows direct migration of the larva. Occasionally an adult infects the body cavity, perhaps because the migrating larva did not have direct access to the kidney. In any event, the large reddish colored worm is destructive, as can be seen by the photographs of two minks, one with an infected right kidney (Figures 158 and 159) and the other with worms removed from the body cavity (Figure 160).

The life cycle of *Dioctophyma renale* is rather straightforward (Figure 161), but described improperly in many textbooks. Eggs exit in host urine and embryonate. Specific aquatic oligochaetes ingest eggs with the developed larva; this larva develops further in the worm's ventral blood vessel. Since mustelids, canines, and other carnivores seldom feed on small oligochaetes, most of these mammals depend on paratenic hosts for their infections. Some small fish feeding on the oligochaetes acquire the larva and even support considerable growth, but not maturation, of the worm. The nematode

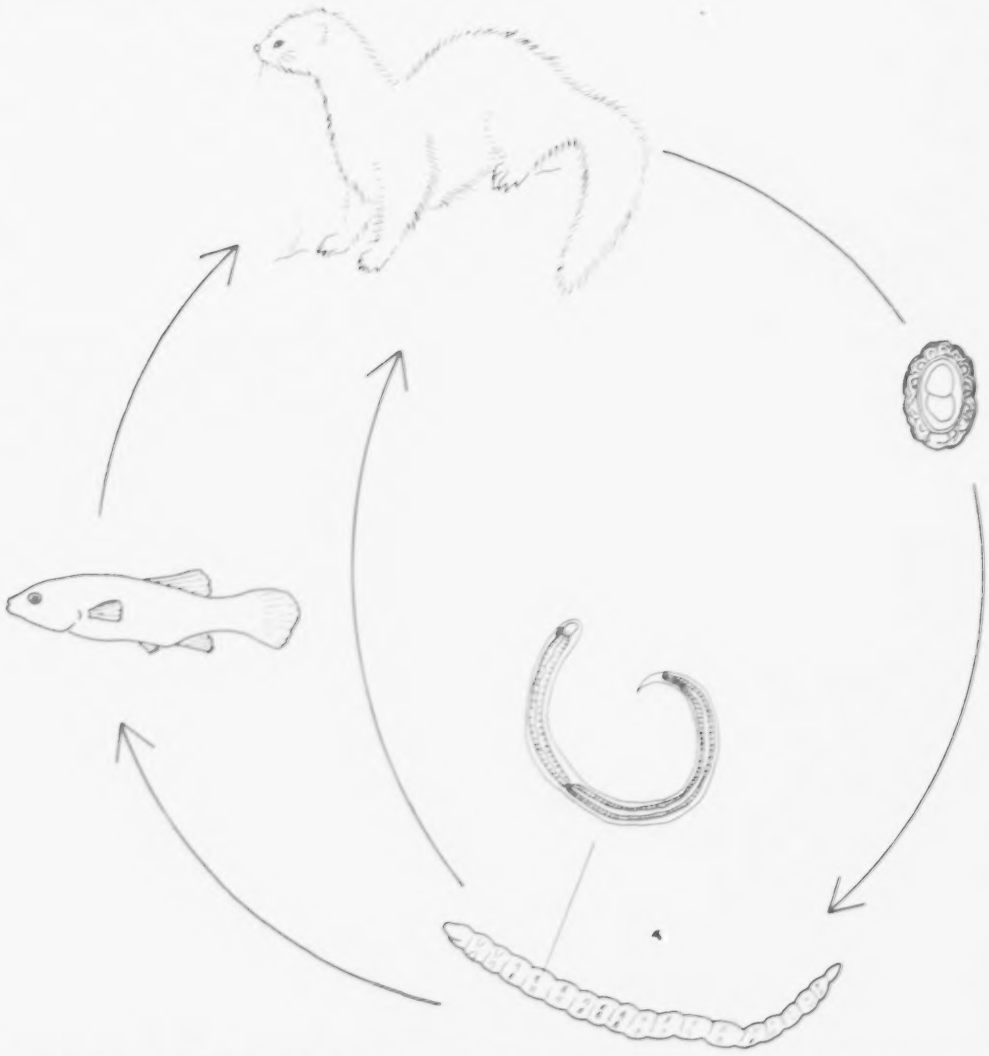


Figure 161. Life cycle of giant kidney worm *(Dioctophyma renale)* of carnivores. A mink or other carnivore acquires an infection by eating any of several, minute, aquatic, free-living worms or more often by eating a fish that has eaten one of those worms. Once in the mammal, the worm typically migrates to the right kidney. It penetrates into that organ and devours all the tissue, growing to over a meter long, if the animal has a large enough kidney. Eggs are deposited with urine and after a short developmental period are infective to the aquatic worm.

can grow many times longer than the oligochaete once in a fish.

Even though primarily a freshwater disease, I have seen several wormy mink that had been trapped from estuarine marshes in Louisiana, including those photographed.

Most large reddish-colored worms encountered in both fresh and estuarine fishes, however, are not the kidney worm, but close relatives (*Eustrongyloides* spp.). Eustrongyloids appear similar except the female has her genital opening in the posterior end rather than anteriorly. Adults infect the intestine, stomach, or proventriculus of herons and some other water birds. In a few birds, they embed in the stomach wall, partly degenerate, and produce an abundance of eggs. In others, they inhabit the intestine without apparent harm to the host. The life cycle is the same as that for the kidney worm.

84.8

Eustrongyloids penetrate out of the flesh of dead infected paratenic hosts. Striped bass maintained in a pond at GCRL as well as mosquitofish, killifish, and tadpoles all had worms escaping after a large scale mortality in the pond. Whether the worms had any influence on the mortalities was not established, but investigating the relationship would be a good problem. Striped bass held in aquaria and fed gambusia acquired larval *Eustrongyloides* sp., whereas others not fed fish did not, suggesting the ability of the worm to be maintained by a series of paratenic hosts.

Larval eustrongyloids have been implicated in deaths of herons and egrets. Actually, when a variety of birds feed heavily on infected fish, death can follow. Numerous red-breasted mergansers in Virginia died a day or so following engorgement on infected mosquitofish and silversides trapped beneath a thin sheet of ice on a brackish pond. Migrating worms reduced the birds' liver, proventriculus, and air sacs to a bloody pulp.

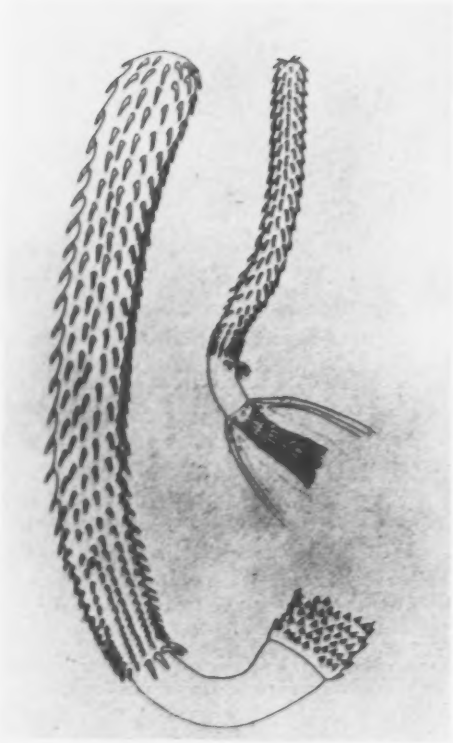


Figure 162. Proboscises of juveniles of two related thorny-headed worms (acanthocephalans). Large one on left is *Tegorhynchus furcatus* that commonly infects the southern kingfish, and the smaller one is *Dollfusentis chandleri* that commonly infects the Atlantic croaker. Even though both can be transmitted by amphipods from near high salinity beaches, *Dollfusentis chandleri* usually infects estuarine hosts that feed on amphipods from low salinity habitats.

Thorny-headed Worms

Acanthocephalans, or thorny-headed worms, are all parasitic, even though living worms presumably shed from fish do occur in benthic samples. They look superficially like roundworms. Actually, they have no gut, they have a protrusible proboscis with hooks, and their reproductive and most other systems differ considerably from those of roundworms. They, like roundworms, have separate sexes.

Several different species occur in local fishes. The sheepshead minnow hosts one *(Atactorhynchus verecundum)* and the cobia (= lemonfish) hosts another *(Serrasentis sagittifer)*. In order to see the first species, a microscope is necessary, but the latter species stands out conspicuously when one cuts into the intestine and pyloric caeca of a cobia because it frequently grows longer (but substantially narrower) than a finger. Many other species occur commonly, even in the fresh-brackish water interface where one *(Leptorhynchoides thecatum)* infects most members of the sunfish family as well as a variety of marine intruders. An orange-colored species *(Pomphorhynchus bulbocolli)* may make a stronger impression on an observer from this low salinity-freshwater habitat because its bulbous proboscis permanently embeds in the gut of the bowfin (= mudfish, *Amia calva*) and a few other fishes.

As an extremely common estuarine example, *Dollfusentis chandleri* portrays a characteristic thorny-head (Figure 162). This species infects the rectum of the Atlantic croaker, spot, and a variety of other fishes. It is quite similar to a larger species *(Tegorhynchus furcatus,* Figure 162) which embeds in the intestine of the southern kingfish (= ground mullet, *Menticirrhus*

Figure 163. Typical example of a nearly mature acanthocephalan egg. The shell of most species looks like a diatom and thus a source of food for the arthropod intermediate host. The nearly infective acanthor can be seen inside the shell.

americanus) and a few other fishes. In both cases, many individuals can infect a single host. Indeed, over 450 specimens of *Dollfusentis chandleri* crowded into the rectum of a relatively small (as long as a hand) Atlantic croaker without any apparent harm to the host.

Life cycles show one basic pattern, whether for species infecting fishes or other vertebrates. Developed eggs are sorted and shed by the female worm; they leave the host with its feces. Aquatic ones look similar to a diatom (Figure 163) and consequently simulate a food source for arthropod intermediate hosts. After being eaten by the proper arthropod, the larva (acanthor) forms another stage (acanthella) which gradually develops into an infective juvenile. Finally, the arthropod with the worm is eaten by and the worm infects the proper vertebrate host. In the case of acanthocephalans from fishes, most either use an ostracod or an amphipod host, but few use copepods, isopods, and other hosts. Since the cobia and many other host-fish do not feed on such small crustaceans, the reader may wonder how the cycle is completed. Once again, the paratenic host becomes a vital link in those cycles. Consequently, some biologists call the host a transfer host. Fish usually fill this role and, in the case of *Serrasentis sagittifer* which matures in the cobia, the Atlantic croaker, inshore lizardfish, lane snapper, and other fishes function as the transfer hosts by harboring juveniles (cystacanths) in their mesenteries.

Dollfusentis chandleri (Figure 164) does not need a transfer host in its life cycle because its definitive hosts eat amphipods. A few unrelated amphipods from habitats ranging from nearly-fresh to full-strength seawater can host it (reported from *Lepidactylus* sp., *Grandidierella bonnieroides*, and *Corophium lacustre*). Up to three cystacanths, each folded over on itself and longer than the amphipod, can inhabit the same host (at least for the closely-related *Tegorhynchus furcatus* in *Lepidactylus* sp.). *Tegorhynchus furcatus* appears to cause an increase in the host's size; evidence suggests infections may even make the affected amphipod a more accessible item of prey.

Most croaker usually acquire *Dollfusentis chandleri* in low salinity bayous about early summer. The worms can remain in this principal final host for over a year, but females usually restrict egg-production to a short period sometime in or near summer. Unlike many acanthocephalan species, males and females remain in equal numbers. Many species of both acanthocephalans and nematodes undergo a loss of males following fertilization, but this acanthocephalan acts as an exception.

Crustaceans

Crustacean parasites from fishes evoke more interest than most parasites because they are readily visible and show such a wide variation in appearance. Isopods can be extremely large and fierce-looking, whereas copepods come in all sizes and shapes. Both groups have large numbers of nonparasitic relatives. The parasitic ones have evolved several features to assure their livelihood. Some have evolved to the point where, without examining larvae and mouthparts, one could hardly classify them as crustaceans.

Crustaceans have a protective, external, nonliving cuticle which sheds during maturation. This molting process was described earlier in conjunction with crab symbionts. Most parasitic crustaceans also possess a variety of appendages the same as nonparasitic ones (see figure 48 of a brown shrimp).

Structures of the isopod *(Lironeca ovalis)*

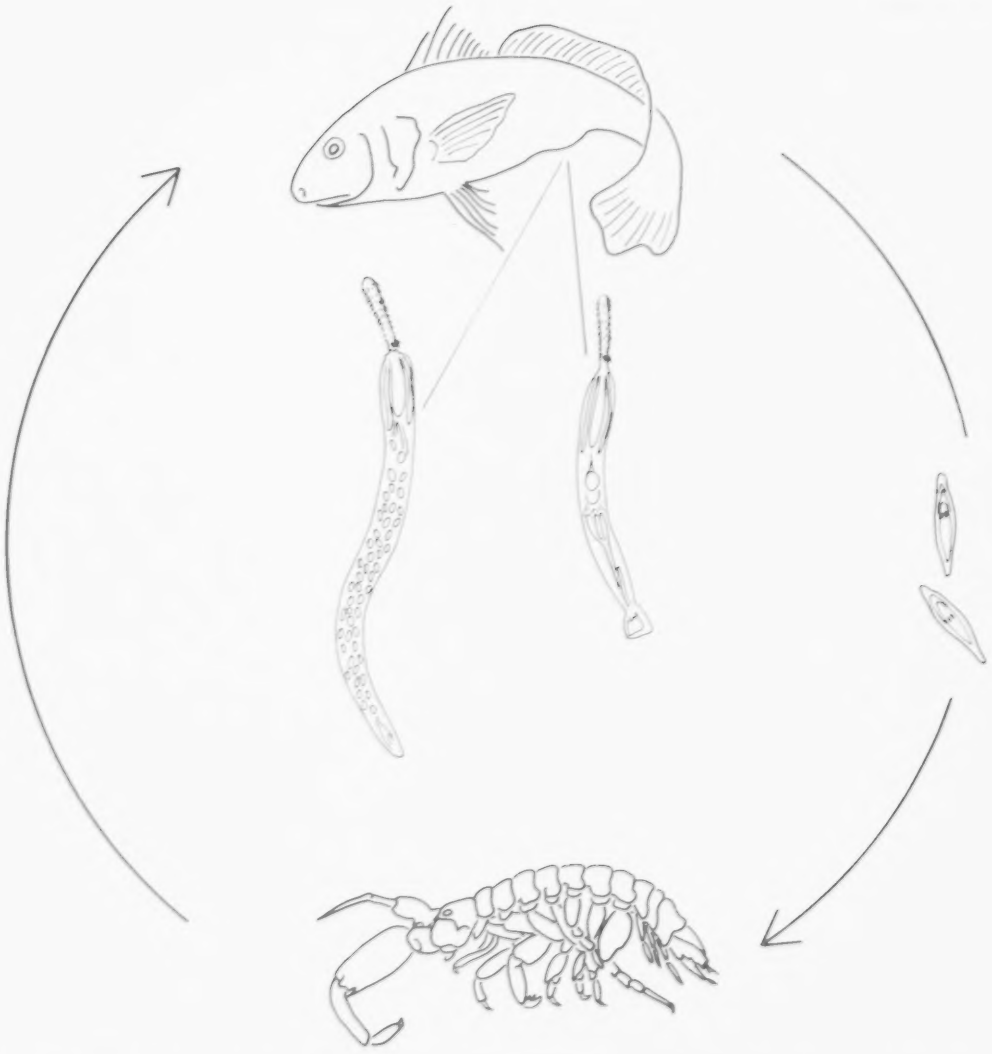


Figure 164. Life cycle of acanthocephalan *(Dollfusentis chandleri)*. Male and female worms live and mate in the rectum of the Atlantic croaker and other fishes. Specific amphipod crustaceans feeding on deposited eggs acquire a stage that ultimately produces a juvenile worm. Croaker become infected from eating these amphipods; however, some other acanthocephalans utilize different arthropods as hosts, and some use additional transfer hosts to bridge the apparent gap between an arthropod and a predator that feeds on relatively large prey.

most commonly observed on the gills of a variety of fishes have been modified much less than those on the bopyrid discussed earlier from under a grass shrimp's carapace (see Figures 82 and 83). Effective claws, however, do hold that asymmetrically shaped parasite to the gills or adjacent regions of its fish-host. Oftentimes, most of the filaments from several gills erode away and secondary infections ensue (see discussion on bacteria and lymphocystis). When one isopod infests each side of a host, the debilitation must be considerable. Three views (Figures 165 to 167) illustrate a sheepshead with two such unwanted "passengers."

Some other isopods display themselves more conspicuously when a host dies. Occasionally a large percentage of a stock of Gulf menhaden (pogy) will have a large species *(Olencira praegustator)* attached to

Figures 165-167. Three views of a young sheepshead with an isopod (*Lironeca ovalis*) in each gill chamber. Top, side view. Middle, top view showing bulge. Bottom, ventral (underside) view showing protrusion. Normally, the opercula do not protrude from body.

the roof of the mouth. Actually, that is the female; smaller males and juveniles feed on the gills, but can occur in the mouth. All these come crawling out on the deck or sorting tray of a fishing boat as the fish die. Some evidence suggests that many infested or otherwise injured menhaden cannot function with their normal school and therefore recuperate by swimming with slower younger schools or remain near shore during summer and fall.

The isopods situated in the oral cavities of pigfish and southern kingfish take more effort to find than simply opening the mouth as in menhaden and some other fishes.

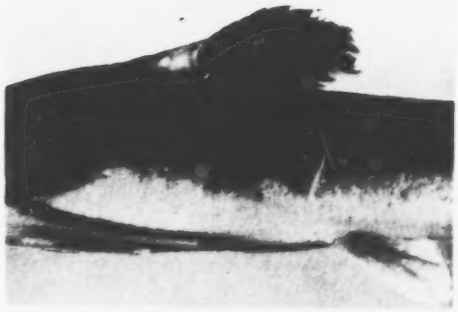


Figure 168. An isopod (*Nirocila acuminata*) attached to the dorsal fin of the sea catfish. The same isopod commonly infests the tail and also the fins of a few other fishes.

Externally-located species gain the attention of divers in clear tropical waters. An infested sergeant major in Panama or a squirrelfish in the Virgin Islands stand out obviously. Actually, a striped species *(Nirocila acuminata)*, common on sea catfish and remoras, is just as conspicuous (Figure 168) in the northern Gulf. Apparently these may stay attached for long periods because a small fish has a small isopod and a large fish has a large one. A species *(Anilocra acuta)* on the spotted gar either debilitates that host considerably or selectively infests an already weakened fish. Sick fish with extensive lesions associated with the isopod, especially on or near the bases of their fins, can be picked out of the water with bare hands or a dip net.

The life cycle for most of these isopods has not been investigated. Whereas a few species may not utilize an intermediate host, most do, and different species of fishes apparently act as those hosts for several species. In the Bahamas, nearly 100 tiny immature isopods can be seen crawling about on the skin of a moderate-sized grouper. Intermediate hosts for most species harbor fewer larvae. Presumably these larvae do not mature until attaching to the next proper host. In the Gulf, the immature form called *Aegathoa oculata* probably represents several different isopod species. Usually just one or two of these large individuals infest a single host.

Copepods evoke curiosity because of their range of modifications. Indeed, two evolutionary lines of nonrelated copepods have counterparts that superficially resemble each other. These lines range from looking

Figure 169. Adult caligid copepod from gills of sheepshead. The view shows the underside (ventral aspect) with the egg sacs trailing posteriorly.

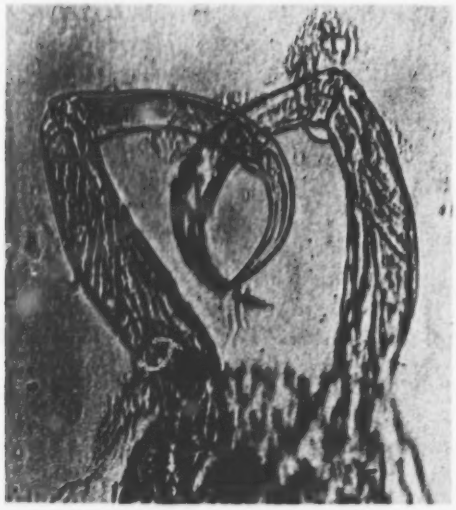


Figure 170. Modified antenna of female *Ergasilus* sp. used for clinging to the gills of its host. A variety of species infests estuarine Gulf species.

nearly like free-living copepods to looking like blobs.

A large number of copepod species infests fishes in the northern Gulf, but only a few will be mentioned. Easy to see on the skin of the southern flounder, sea catfish, and a variety of other fishes including the Atlantic croaker, a transparent copepod *(Caligus praetextus)* presents a common example of a non-permanently attached copepod. The copepod scampers about actively in large numbers when the host is pulled out of the water. Sharks have other copepods (pandarids) which can be spotted because of their brownish cast against the greyish-colored hosts. These copepods also have little corrugated padlike objects on their limbs. The mature females of the caligids, pandarids, and most other copepods can be quickly separated from the males because the females have long posterior egg sacs (Figure 169).

Members of another family of copepods (ergasilids) look like free-living species except the antenna of the female is modified into a powerful prehensile grasping organ (Figure 170). The antennule remains as a sensory structure. These small female parasites, without their mates, can be seen clinging by their pair of antennae to the gills of many Gulf fishes as well as freshwater species. Mullet and killifish both act as prime hosts for observing specimens. Since the mullet is larger, hundreds of the white specks binding to the bright red gills presents a conspicuous spectacle. They can damage their hosts by digesting and rasping mucus and tissue from the gills. Pond-reared hosts appear more vulnerable to mortalities; striped mullet in their normal habitat often have most of their gills covered without showing any obvious ill effects. Possibly fewer secondary infections occur in wild fish than in pond-reared individuals. Ergasilid copepods probably attach to other species of copepods as intermediate hosts.

A common species *(Lernaeenicus radiatus)* that looks nothing like those mentioned above infests a wide variety of local fishes. Its anterior end extends into the host's flesh so that its head, which forms antler-like appendages, can cling around a vertebra or some other structure adjacent to a rich blood supply. Blood appears to be a primary food source. The head structure varies according to where and how it attaches. Without carefully removing this internal portion, a confirmed identification is impossible. An observer still clearly sees

the long neck, body proper, and egg strings which change in color from transparent to reddish-brown as the larvae (nauplei) develop. Red blood from the host can also be observed flowing back and forth within the external body.

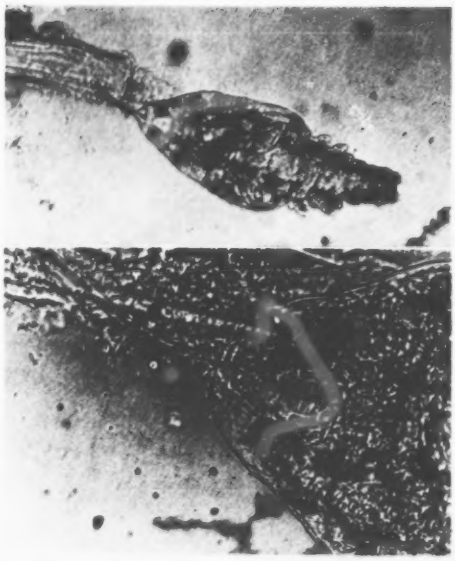
During specific years, the Gulf menhaden has heavy infestations of *Lernaeenicus radiatus*, whereas in other years, one or more species of anchovy show up heavily infested. During most years, a few croaker, seatrout, killifish, gobies and others may turn up with an embedded worm or two. In the case of *Lernaeenicus radiatus*, the rock seabass, primarily in high salinity water, harbors the larval stage (chalimus) attached and free on its gills; thus the abundance of the seabass governs the ultimate number of adult infestations in other fishes. Obviously, the adult parasites can kill their hosts if vital organs are disturbed or if too many individuals infect a host.

In addition to being able to harm the host, *Lernaeenicus radiatus* is itself vulnerable to undesirable symbionts. Figure 171 shows a hydroid attached to and presumably killing one of two individuals.

A few related copepods occur on mackerel and other fishes. Examples from other geographic regions are also well known. One from a whale grows about 60 cm (2 feet) long, and Eskimos feed on another from the gills of the Atlantic cod that has a body-proper about 5 cm (2 inches) across.

The Florida pompano acts as an intermediate host for an unidentified chalimus (Figures 172 and 173). Note the frontal

Figure 171. Two specimens of a copepod (*Lernaeenicus radiatus*) embedded in the bay anchovy. The anterior individual, however, has been totally encrusted with a hydroid.



Figures 172 and 173. Larval copepod (chalimus stage) on tip of Florida pompano's fin. Top, entire view. Bottom, close-up of frontal filament that attaches copepod to host.

filament of the copepod attached to the fin of its host. Fertilization often takes place at this stage when a male breaks the filament and finds a female. The female will then break away and it or both male and female infest the gills or flesh of the proper definitive host. When a chalimus infests a larval or juvenile fish, as it occasionally does, it probably makes the host more vulnerable to predation.

Many other weird-looking copepods can be seen on local fishes. Look at the gills of a redfish or black drum for the experience of trying to decipher what kind of organism is present. (It may be *Lernanthropus longipes.*)

Parasitic copepods constitute an important dietary source for some "parasite pickers." A variety of fishes and shrimps have evolved behaviors allowing them to feed on monogeneans, crustaceans, dead tissue, and other items that could potentially aggravate the host if not removed. Some of these pickers feed exclusively on parasites, whereas others do not. Most popularized pickers display bright colors and inhabit tropical reefs; however, juvenile sea catfish and some cyprinodontid fishes appear to pick material off local fishes. Also,

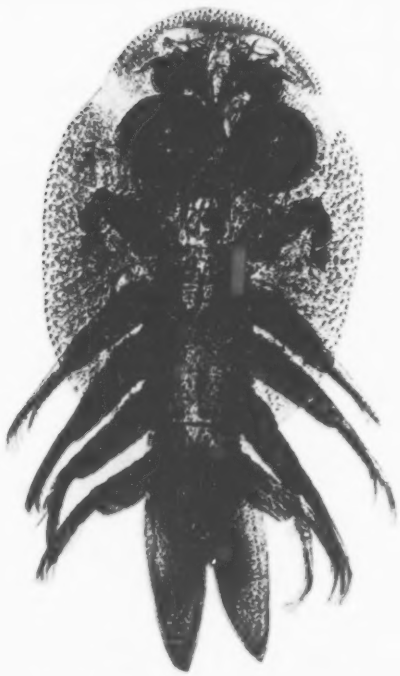


Figure 174. Argulids such as the one shown here have acquired the common name "fish lice." They are not copepods. Note the two compound eyes and cuplike suckers modified from mouthparts. Eggs are laid in strings rather than carried like copepods, and argulids can damage their hosts.

some diskfishes eat parasitic copepods off their primarily pelagic hosts.

Another external crustacean that appears superficially like a caligid copepod, but belongs to the Branchiura group, often goes by the name argulid or "fish louse" (Figure 174). In the typical argulid figured, note the compound eyes and the modified mouthparts forming two disks. This attractive little disk loses most of its intrigue when it reproduces in an aquarium. Females lay eggs on a hard substratum and development of young ensues without intermediate hosts. Quickly, the piercing stylet, or "sting," and proboscis of these active young symbionts can overpower aquarium fishes, occasionally producing an ulcerated depression where the argulid can reside.

When snorkeling among a school of Florida pompano, a diver might think his eyes are playing tricks on him. Are small brownish specks moving about on the sides of some of the fish? They are real! Actually, the colored dots are an argulid (*Argulus fuscus*), occasionally numbering up to a dozen per fish and involving about 10 to 30% of the pompano and Gulf kingfish among the breakers along the Mississippi barrier islands and northwestern Florida beaches.

Some species show more host specificity than others. An exceptionally large species (*Argulus funduli*) infests the relatively small killifish, a smaller one (*Argulus lepidostei*) occurs in large numbers on the spotted gar, another small one (*Argulus flavescens*) commonly infests the southern flounder and several other fishes, and several other species also infest local fishes.

MISCELLANEOUS HOSTS

The American Alligator

The establishment of an alligator season in Louisiana made several large parasites more accessible to hunters and other interested people. If interested, one could probably see four ascaridoid nematode species in the stomach, a variety of digeneans from several families in the intestine, a pentastome (*Sebekia oxycephala*) in the lungs and liver, and a large leech (*Placobdella multilineata*) on the skin and in the mouth. The leech acts as an especially good indicator that the infested gator was from or had recently resided in freshwater. Actually, most of the gator's parasites are acquired in freshwater, but some come from brackish water (*e.g.*, the acanthostome digeneans). All the major groupings have been discussed previously except the pentastome, or tongue-worm, which belongs in a separate phylum.

Pentastomes have arthropod-like nymph larvae. Adults possess four powerful anterior hooks (Figures 175 and 176) used for embedding their mouth region into host tissues. They feed on tissue-fluids and blood cells. The nymph of the alligator species (*Sebekia oxycephala*) infects a variety of fishes. Even though not parasitic to man, its relative from rattlesnake lungs has a nymph that can infect mice, and that nymph could potentially infect man.

Pentastomes typically infect the lungs of

Figures 175 and 176. A pentastome (*Sebekia oxycephala*) from the lungs and liver of the American alligator. Forming a group of their own, pentastomes produce young nymphs that infect an intermediate host. The one from the alligator develops in a fish. Most pentastomes mature in the lungs of reptiles. Top, anterior side view. Bottom, anterior frontal view of a chemically cleared specimen.

reptiles. An exception (*Reighardia sternae*) infects the air sacs and body cavity of local gulls and terns. This bloodfeeder may bypass an intermediate host and infect the bird directly.

Birds

As the reader may suspect, birds harbor many members of the same groups of parasites as do the other mentioned hosts. I noted above that the air sacs are a site for pentastomes. Several nematodes and digeneans also infect these sacs, but other species additionally infect a number of sites not present or seldom infected in fishes,

Figure 177. A mating pair of feather mites from a royal tern. Some species cause their hosts to deplume themselves.

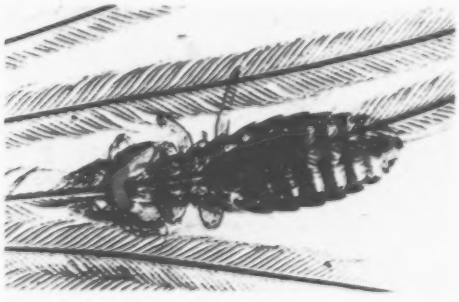


Figure 178. Feather louse on breast feather of clapper rail. Lice are generally quite specific to their bird hosts and those from marine birds do not cause human disease.

including the conjunctival sac of the eye, bursa of Fabricii, and kidney.

Shore, marsh, and marine birds host a variety of parasites that do not infect fish; most of these are arthropods: nasal mites, feather mites (Figure 177), hypopial mites from subcutaneous tissues, lice (Figure 178), and others. Fleas and ticks seldom infest aquatic birds.

Just the thought of lice and other arthropods crawling over a person handling an injured or dead bird may cause itchiness. Actually, even the bird-handler who frequently contacts birds seldom receives a rash

from handling aquatic or marsh birds. A few arthropods on non-aquatic birds do cause rashes. The tropical fowl mite (*Ornithonyssus bursa*) from the English sparrow occasionally bites man, causing a rash (dermatitis). That mite, however, cannot live longer than 10 days without the sparrow or a few other domestic fowl which can host it. Chiggers, or "red bugs," also cause irritation, but seldom infest aquatic hosts.

Searching for avian arthropods can be fun. Try looking for eggs of feather lice attached to the feathers. The female of these biting lice usually lays her eggs in rows on flight feathers safe from regions reachable by the bird's bill. After 3 or 4 days of development, the nymph molts and undergoes growth for about a month at which time the adult emerges. Some species feed directly on feathers whereas others puncture the quill to take blood and central pulp.

Lice reveal much about a host. If many individuals infest a bird, it is probably so weak that it cannot keep them in check by preening. The lice then can irritate and weaken the bird further. The number of individuals on a healthy host seldom varies throughout the year like it does for many worms. Often several species of lice infest a single bird. The color of these usually varies directly with the color of host; dark colored lice infest dark colored hosts and so forth.

The reason for so many species of lice has been thought to reflect evolution of the group spreading to a variety of unutilized ecological niches* during the period when birds first evolved. Apparently, ancestral lice lived in trees and later started eating tissue-debris on reptiles. As feathers evolved from the scales of reptiles, more habitats became available for rapid speciation of these lice. Some later spread to mammals.

Lice also seem to indicate evolutionary patterns of their hosts. Birds evolved rapidly, so rapidly that few traces of the primitive arrangements of bones and muscles remain, and few fossils exist for birds during this period when the fundamental changes occurred. The fragile nature of the bones of birds is not conducive to fossilization. Since so many lice species infest birds and since they show considerable specificity toward a single species or group of birds, one can speculate with some assurance that both birds and their lice have often evolved together. Since little about bird evolution can be deduced positively from modern evidence, that evidence provided by parasites becomes especially important. Evolution of lice should parallel and reflect that of birds. As an example, flamingos have been placed with storks and herons. Some species of feather lice on flamingos, however, have relatives that occur elsewhere only on swans, geese, and ducks. Lice on storks and herons show no relationship to any of the lice on the other indicated birds. Apparently the ancestors of the duck-lice were present before a common ancestor gave rise to flamingos and modern ducks. Thus, maybe flamingos should be placed more closely with ducks than with herons!

Some biting lice also seriously harm their hosts. Juveniles of the white pelican and double-crested cormorants in their rookeries may be killed by a species (*Piagetiella peralis*) that heavily infests the oral cavity. Attached to the tissue of the pouch and roof of the cavity, over 500 of these 3 to 6 mm long, transversely-striped lice can cover most of the mouth's available space. Additional immature forms occur elsewhere on the body surface. Young white ibis in rookeries also host a troublesome biting louse. Secondary bacterial infections (*Staphylococcus* sp.) often accompany the louse infestation, and an infected young bird looks as if it has mange. The host-parasite balance between young of nesting aquatic birds and their arthropod symbionts needs further investigation.

A final comment on bird parasites concerns white patches commonly found in the breast of surface-feeding ducks, but also in birds from at least 21 other families. These cysts infect heart, leg, and neck muscles, and they are all the same species (*Sarcocystis rileyi*). A definitive host for this coccidian protozoan has not been determined, but it is possibly a raptorial bird or carnivorous mammal. A related species in the muscles of a cow utilizes the intestine of man or dog as a final host.

Marine Mammals

Marine and estuarine mammals harbor a multitude of parasites, and the discussion for most, just like for most birds, is beyond the scope of this guide. Because of the pleasant and almost humanoid nature of the Atlantic bottlenose dolphin and the fact that this porpoise commonly makes its presence known in the Gulf, a few comments on some of its parasites seem warranted. The federal government protects marine mammals, even when dead, reducing the chance of seeing their internal parasites. The penetrating odors transmitted with oils in the blubber make cutting into a beached mammal dead only a few hours a rather unpleasant experience, anyway. If some inspired person in the northern Gulf does get the opportunity to see a fresh stomach lining of a porpoise, he would probably see two species of digeneans and possibly a mass of nematodes. Large numbers of a rather strange looking fluke (*Braunina cordiformis*) about the size of a marble attach firmly to the stomach and can live for up to 3 years. The other digenean (*Pholeter gastrophilus*) is smaller, but cannot be seen because a nodular cyst larger than the previous fluke forms around the worm and hides it. The nematodes belong to one or more species of *Anisakis*, the larvae of which when present in raw seafood have been implicated in severe human gastric disease. Its life cycle was diagrammed earlier (Figure 157).

A few other worms commonly infect the porpoise. One elongated fluke (*Nasitrema delphini*) inhabits the lateral air sinuses of the head near the internal ear. Less commonly, a campulid fluke species infects the pancreatic ducts. The reason for mentioning this infection is that worms in this family have been implicated in some strandings of marine mammals.

Several dolphins that had stranded singly along California beaches had livers badly damaged by a campulid and had extensively damaged brains apparently resulting from easily diagnosed campulid eggs. Eggs and occasionally adults pass through the pancreatic duct and ultimately invade various tissues including the brain, causing them to degenerate. A few nematodes can also invade the brain.

A lungworm (*Halocercus lagenorhynchi*) inhabits the air passages of the lungs. This nematode may cause severe bronchitis. Possibly because an infected porpoise has a poorly developed cough reflex, it cannot discharge resulting fluid. A healthy porpoise seems able to control the parasite, but a very young or stressed host apparently often allows numerous individuals to mature and thereby contribute to its death or a serious disease. A heavy infection of a related worm in the auditory capsule can cause deafness.

Conspicuous to someone admiring the antics of the bottlenose dolphin alongside his vessel are the skin disorders of some individuals. Cuts and sores from fishing nets, shark attacks, or even self- or peer-induced trauma may progress into debilitating infections. When a dominant porpoise bites its subordinate companion, the rake marks of its teeth orient parallel (Figure 179). Many animals also show a variety of healing wounds, often with secondary infections (Figure 180). Other types of lesions occur on the skin. Some

Figures 179 and 180. Lesions on the Atlantic bottlenose dolphin. Top, flipper with deep wounds made by another dolphin. Bottom, secondary infection of wound in dorsal fin.

result from bacterial or fungal infections and the cause of some remains unknown. People who work with porpoises refer to some common dark colored patchy lesions as "tattoos." These do not appear to harm the host, but their cause should be investigated.

Because marine mammals reach gigantic sizes, a reader might expect a gigantic worm to infect large whales. One exists! Blue and fin whales have a nematode (*Crassicauda* sp.), the males of which occur in the penis or clitoris. The much larger female worm extends from this region down the ureter, through the kidneys, into blood vessels, and occasionally to the liver. This is a long worm.

MISCELLANEOUS SYMBIONTS

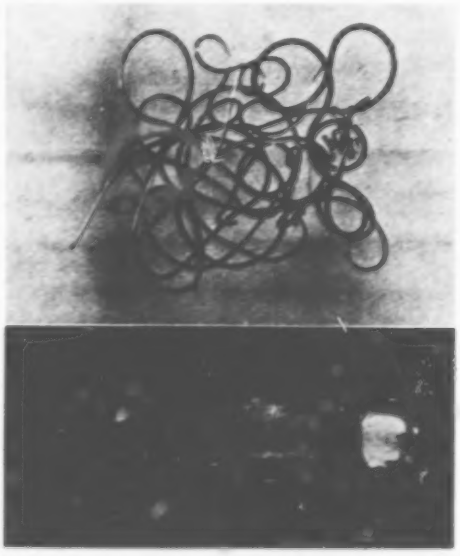
Nematode larvae and larval nematode-like organisms infect insects and other hosts in addition to fish and the mentioned shellfish. Because people can see these worms, they deserve some comment.

Fairly common large nematode larvae in insects may be mermithids. If so, farmers refer to them as "cabbage snakes." The infected midge in Figure 181 from an estuarine bayou exemplifies a local infection. Spiders, leeches, crustaceans, and other invertebrates harbor specific mermithid larvae, some of which reach 50 cm in length. Because they have life cycles adapted to their specific hosts, produce large numbers of eggs, and are free-swimming or otherwise readily available to infect the hosts, some act as good agents for biological control of pests.

In order to appreciate better these potential biological control agents, I present a brief life history of one (*Perutilimeris culicis*) from the saltmarsh mosquito. Free-living females lay thousands of eggs in the substratum, and the small preparasitic larva hatches and penetrates an early instar* mosquito larva. It does not grow, but remains dormant until the mosquito pupates. At that time, the larva migrates to the abdomen and enlarges rapidly soon after the mosquito matures and obtains a blood meal. The host becomes sterile and then dies when the internal postparasitic stage with its lance-like tooth perforates an escape hole. Once in the water, the nematode molts, mates, and lays eggs. Some other species produce eggs that must be eaten and larvae that enlarge in the larval insect host.

Not to be confused with mermithids, but also infecting insects and other arthropod

Figure 181. Mermithid roundworm abandoning a midge larva. Mermithid nematodes have a parasitic larva which in some cases acts as a biological control agent to keep populations of annoying insects under check.



Figures 182 and 183. A horsehair worm (*Gordius robustus*). Top, several males that had been found wiggling together in a shallow pond. Juveniles parasitize grasshoppers and a variety of other hosts. Bottom, posterior tip of a male worm. The female of this species has a rounded rather than a lobed tail.

hosts are immature "horse-hair" worms (Figures 182 and 183). These nematomorphs, or gordiacean worms as they are also called, appear superficially like long dark-brownish nematodes. The digestive tract is vestigial in nearly all species, and adults do not feed at all. Juveniles secrete digestive enzymes through their tegument and absorb host-nutrients directly back through their body with little damage to the host. Development occurs gradually from larva to juvenile without metamorphosis. When someone sees a larva in a grasshopper, or an adult in a water trough or in their yard, some unnecessary anxiety usually develops.

A few marine parasitic nematomorphs exist; one (*Nectonema agile*) even infects the hemocoel of a grass shrimp along the northeastern United States coast in which it reaches at least 10 cm in length. The ovaries of females with ova shrink and become opaque, but the host is not killed. Horsehair worms that I have seen in the northern Gulf belong to a freshwater species (*Gordius robustus*), even though some individuals occur in brackish areas. The specimens have all been encountered during early winter and summer, but they can probably be found during most warm months. A juvenile worm emerges from its host while in water, becomes sexually-mature, and mates; the slightly mobile females occur in grassy regions or in water near shore, whereas about an equal number of males swim actively in the deeper adjacent regions or wiggle in the grass. The male appears to search out the female. After the ova are fertilized, the female lays strings or masses of eggs. When a larva hatches from the egg, it penetrates any of a variety of hosts and undergoes its entire development as a parasitic stage. If not in a proper host, it may encyst. If a person or fish eats an infected host, the larva may develop, usually without damage to the new host.

A few symbionts have been mentioned because they can be maintained alive with little effort when separated from their hosts. The ease with which one can collect polyclad flatworms from oysters, barnacles, and other hosts for study or observation exemplifies this. A related triclad flatworm

Figure 184. A commensal triclad flatworm (*Bdelloura candida*) from base of leg of the horseshoe crab. Note the eyespots anteriorly, the large protruded feeding pharynx near the middle, and the adhesive holdfast organ posteriorly. Separated from the host, these worms can be kept alive for extended periods with liver or other sources of nutrients.

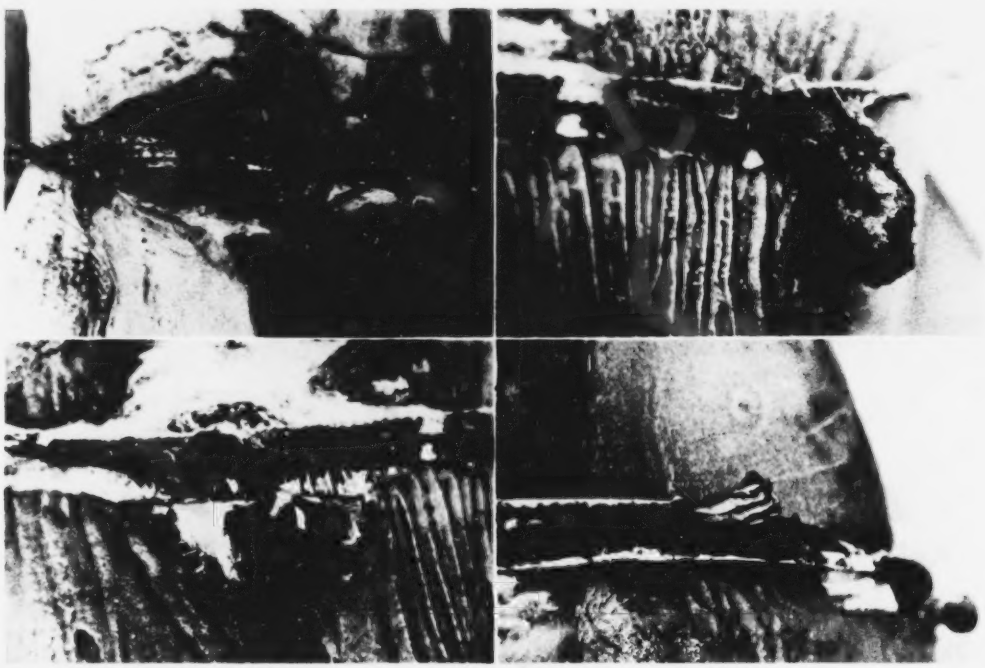
Figure 185. A large tuberculated leech (*Stibarobdella macrothela*) on the anal fin of a large bull shark. Commonly encountered on sharks, it also occurs on other animals and substrata in high saline waters. The photographed specimen had been preserved and lost its greenish-grey coloration. Note the encircled area where the large posterior sucker had attached to the fin.

(*Bdelloura candida*, Figure 184) is also an inviting organism to study. This large worm can be found on most large specimens of the horseshoe crab (not actually a true crab) by looking where the legs attach and at the book gills (named because the leaf-like lamellae on the breathing appendages suggest a book).

Leeches have already been mentioned as symbionts infesting the blue crab and shrimps and as a vector of blood parasites. Even though several other leeches occur in the northern Gulf, one (Figure 185) deserves attention because of its large size and its elasmobranch hosts. The tuberculated leech (*Stibarobdella macrothela*) can reach a length of about 15 cm, but most measure about 3 cm long. It typically infests the mouth, fins, claspers, and skin of any of several sharks, as well as of the guitarfish, crabs, shells, and occasionally bony fishes. It occurs worldwide in high saline habitats.

Figure 186. Medium-sized dusky shark encircled by a commercial plastic packing band. Barnacles attach to the band.

Barnacles have already been discussed as symbionts showing various degrees of association with crabs. Barnacles also attach and have commensal relationships to other living organisms, but often they attach because the organism acts as a solid substratum rather than a symbiotic partner. Three species that attached to a plastic band around a shark demonstrate this. Two dusky sharks off Pensacola, Florida, became encircled within commercial plastic packing bands (Figure 186). A close-up



Figures 187-190. Barnacles attached to plastic packing bands encircling the dusky shark. Top left, note the damage caused the shark at its gill slits, structures through which water passes so that the shark can obtain oxygen. Top right, a common gooseneck barnacle *(Lepas anatifera)* covered by a filamentous green alga. Bottom left, the rabbit ear whale barnacle *(Conchoderma auritum)* which often attaches to sessile barnacles on whales. Bottom right, rare in the Gulf, another related barnacle *(Conchoderma virgatum)* often attaches directly to fish and their parasitic copepods.

photograph (Figure 187) reveals the damage caused to the body near the gill slits by the band. Similar harm caused to other fishes will be discussed later, and I will focus my attention here on the barnacles. A common goose-neck barnacle (*Lepas anatifera*) frequently attaches to drifting wood and other objects. One individual on the plastic band (Figure 188) had become covered by attached filamentous green algae. Another stalked species (*Conchoderma auritum*, Figure 189) has the common name "rabbit ear whale barnacle" because it has been collected off whales. Actually, many specimens collected during modern times come from hulls of ships that transit tropical and subtropical Atlantic and Mediterranean waters, but their common presence on whales seems more than accidental. Another species (*Conchoderma virgatum*, Figure 190), even though often attaching to ships and flotsam, does attach directly to small living organisms. Not common in the Gulf, it has been reported there from the dorsal fin of a halfbeak and on a parasitic copepod (*Lernaeolophus sultanus*) embedded in the flesh of a cobia. Considering such rare sightings of this barnacle, a rather unique combination of conditions seem to be required for its development. Perhaps one of these conditions is a wound.

Whether one considers as parasites insects that must feed on blood to produce eggs is a matter of individual interpretation and interest. Because biting gnats, even more than mosquitoes, have such a dramatic influence on people's daily outdoor activities, I include a few comments on them.

From a human point of view, gnats (at least *Culicoides furens* and *Culicoides hollensis*), also called "no-see-ums," "punkies," and "sand flies," can vector true parasites and often make collecting parasites or just being outside miserable. One species (*Culicoides furens*) acts as the intermediate host for Ozzard's filariasis (*Mansonella ozzardi*) in South America and the West Indies. Because people in North America have not been found to harbor the thin worm in their mesentery, the gnat in the northern Gulf apparently has nothing to propagate.

Figure 191. Underside of a biting gnat (*Culicoides hollensis*). This large gnat is one of the two common gnats in the southeastern U.S. that breed in salt marshes and bite people. It is most prevalent in March-April and October-November and occurs throughout the day. The other species is discussed in the text.

The two indicated species commonly bite people along the Gulf Coast and Atlantic seaboard. Like mosquitoes, only the female gnat sucks blood. Effects of the irritating bite may persist for days in some people, whereas all symptoms disappear within a few hours for others. Along the northern Gulf, adults of the larger (*Culicoides hollensis*, Figure 191) appear from mid-March through April and also during October and November. They feed heavily throughout the day on people, domestic mammals, and probably other animals. On the other hand, a smaller species (*Culicoides furens*) occurs predominantly from May through September, biting near sunrise and again from about an hour and a half before sunset until after the sun sets. Both species breed among the salt marsh vegetation. Larvae of some other species develop in freshwater habitats and those of one (*Culicoides melleus*) develop in brackish intertidal sandy regions. Fortunately, the coastal Gulf pests transmit no known human diseases.

FISH-KILLS AND MISCELLANEOUS DISEASES

Fish-kills are not restricted to finfishes; they also involve shellfishes. In general, shellfish mortalities present more difficulty

in assessing because the hosts are smaller and more easily overlooked, are more readily preyed upon, and seldom swim to the surface. Several examples of diseases that have not been overlooked have already been discussed in the earlier invertebrate sections.

Fish-kills occur for a variety of reasons. Most cases have not been thoroughly investigated, but residents usually know when to take advantage of them. People fill washtubs with fresh fish following a rapid temperature drop or during certain other conditions.

When water temperature gradually drops during the winter, fish usually have time to acclimate or move into deep or offshore water. When the drop is rapid and when fish are additionally stressed such as by the presence of low salinity water, some fish come to the surface and die. Those that sink to the bottom slowly bloat with gas and rise to the surface after about 2 to 3 weeks when the water has warmed and algae has begun to cover them. When these fish surface, people often worry unnecessarily about another fish-kill not associated with low temperatures. Dying fish or those in a coma make a safe product to eat if cooked and not otherwise contaminated.

Other naturally-occurring water conditions may also provide another source of food for the table. Residents in the northern Gulf call the major condition a "jubilee." The eastern shore of Mobile Bay has gained a reputation for its summer jubilees. Once, when the coastal region was less populated, observers would notify their neighbors about these events; they usually occur just before sunrise. Now it is almost everybody for himself, and biologists seldom hear about jubilees until all the fish are collected. Rarely do animals die unless confined like crabs in traps or sessile like oysters; most become stunned for several hours and make a dip net an easy means to gather them. Apparently a combination of specific winds and tides allows water with a low concentration of oxygen to stratify and to move along the bottom of specific areas. Crabs and bottom fishes like flounders and eels move shoreward and evade this encroaching water mass which soon overtakes them.

Summer kills also referred to as jubilees occur along Bellefontaine Beach and Gulfport, Mississippi. Perhaps the cause of these differs from that for the jubilee in Mobile Bay because the conditions related above do not necessarily coincide with those encountered in Mississippi. Many fish die, but neither involved fishes nor the complete state of the water from jubilees has been investigated. Plankton* blooms have been observed during some of the mortalities. If algal toxins cause the mortalities, perhaps investigators should ascertain if affected hosts can be safely eaten.

Devastating "red tides" result from blooms of a few species of toxic planktonic dinoflagellates (primarily *Gymnodinium breve*). They occur periodically along the west coast of Florida and less often along the western Gulf and perhaps elsewhere. When a red tide occurs, large numbers of fish and invertebrates die, an irritating aerosol occurs throughout the nearby coastal areas, and less often, contact-rashes occur in humans. The noxious tides alarm tourists and residents alike.

The alga secretes a neurotoxin that kills any fish if exposed to a sufficient amount. Fish also die from oxygen depletion resulting from decomposing fish and algae. However, other mechanisms of death seem to occur. Two of these are long term neurointoxication and long term blood disease. Different fishes respond differently, and, consequently, only specific fishes die from a group of several species. As examples, low levels of toxin affect the ladyfish's neurological system and the mullet's blood. The mullet's blood clots slowly and the cells break apart. Resulting deaths usually occur a few weeks following a subsided red tide. Typically one or more fish of either species from a large school under continuous exposure to the toxin exhibits a frenzied behavior and dies while others of the same kind remain normal until they too are terminally affected. Some birds, primarily the lesser scaup, also die following red tides. Perhaps this is because they feed on molluscs which concentrate the algae, and thus the toxin. Man can also show symptoms of mild neuromuscular intoxication following ingestion of contaminated shellfish.

Probably the most common cause of fish-kills in the northern Gulf is oxygen depletion. This can occur naturally after several days of overcast skies. Decreased sunlight reduces photosynthesis* and thereby oxygen production, and this, in conjunction whith the loss of oxygen from decomposing organic material, results in an oxygen concentration too low to support most fish life. Domestic wastes and organic wastes from industrial plants intensify algal blooms and the amount of matter to be decomposed. Consequently, the number of mass mortalities caused by oxygen depletion, especially in harbors and enclosed areas, increases with increased population growth.

Other kills result from fishing practices, toxic materials, and combinations of natural and man-controlled factors. Many fish, occasionally entire catches, may be spilled from seines or "culled" from shrimp catches. Pesticides, herbicides, and chemicals may be accidentally or carelessly introduced into a system and kill organisms.

Several other anomalous conditions might be considered diseases. Unless fish are confined in a rearing facility or in a stressed habitat, most of these conditions are seldom observed. Predators eat most affected fish before their genetic, nutritional, and injury-caused diseases become conspicuous to fishermen; however, a few affected fish can be seen, and I will briefly mention a sample.

Anomalies seen by most shrimpers include albinism, ambicoloration, and reversal of flatfishes. Even though most are congenital defects, some anomalies can be caused by trauma during early developmental stages of the fish. When flatfish develop normally, one eye migrates to the opposite side resulting in both eyes being on the top or ocular side. This side possesses pigmentation which can be controlled to vary in color according to the background so that both predators and prey looking down have difficulty detecting them. The blind underside of the fish lacks pigment and provides a difficult target against the water's reflecting surface for a predator from below.

When fish lack pigments in their normal regions, that is "albinism." Usually some pigments occur on the head or elsewhere and the lack of pigment is patchy. Replication of the eyed-side color pattern on the blind-side of flatfishes is termed "ambicoloration." The hogchoker *(Trinectes maculatus)* in the northern Gulf often has extensive shading or pigmentation on the blind-side, but ambicoloration is infrequent in these and other Gulf of Mexico flatfishes.

Figure 192. Reversal of a fringed flounder. The fish on the right is normal, whereas the one on the left has its eyes on the right side of the body.

Reversal indicates the occurrence of eyes and pigmentation on the usual blind side. A normal (right) and reversed (left) fringed flounder *(Etropus crossotus)* illustrate this condition (Figure 192).

By visiting a fish hatchery where large quantities of fry are produced, one may be able to observe a variety of genetically deformed young fish. In the natural environment, many of these abnormal fish would be eaten. Still, increased heated effluents and pollutants in the environment probably produce an increasing number of abnormalities. In order to investigate that likelihood, eggs and embryos have been examined for chromosomal anomalies. Those of the Atlantic mackerel from polluted New York Bight show a high number of all sorts of chromosomal damage with a tendency for more damage to occur in the more degraded regions.

The striped mullet illustrated in Figure 193 might have been a genetic anomaly, a nutritionally-deprived fish, a parasitized individual, or an individual confronted with excessive stress during early development. A variety of pollutants such as sulfuric acid, herbicides, and pesticides can produce such stress.

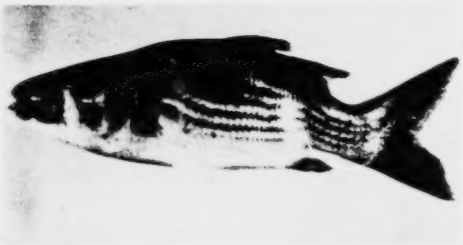
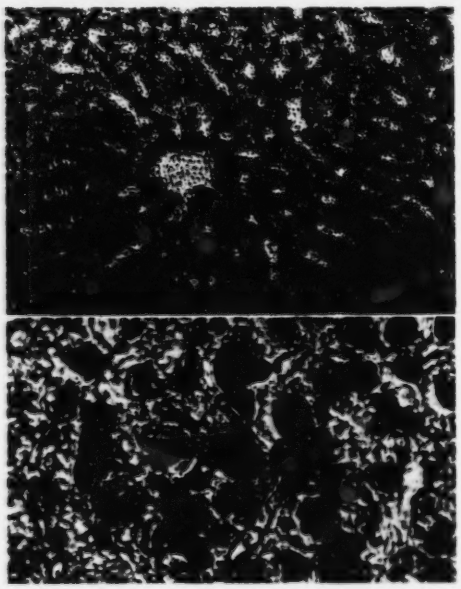


Figure 193. Anomalous striped mullet with sideways curvature of the spine (scoliosis). This condition, usually resulting from a nutritional deficiency, can result from a variety of causes.



Figures 194 and 195. A stained section of fatty liver tissue from the striped mullet. The special stain (Sudan black B) stains the lipid darkly, distinguishing the condition from that of excessive glycogen. Top, double layers of liver cells radiating normally from central vein. Bottom, close-up of large stained fat globules in cells. The condition can be reversed in most instances; excess fat occurs in the liver during starvation, certain vitamin deficiencies, spawning, and a few other conditions. Young fish in aquaria fed exclusively on a diet of a single animal often develop a fatty liver and die.

Fatty livers, livers with cells occupied with lipid material (Figures 194 and 195), commonly occur in naturally starved fish during cold spells, in fish during their spawning periods, and in fish maintained on inadequate diets. Usually the process can be reversed, and the liver will resume its normal character after proper food is eaten. Fatty livers, however, can also result from pollutants.

Figure 196. Fibrous tumors in a striped mullet. This type of growth appears to be increasing in prevalence in polluted estuarine habitats during the past few years.

Some contaminants also induce cancer in fishes and other aquatic animals. So far, in the northern Gulf, few tumors have been reported from fishes. Probably the most prevalent one in estuarine fishes involves fibrous outgrowths in the striped mullet (Figure 196). Usually less than 1% of a catch of fish reveals these externally protruding tumors. They, however, have been seen only in polluted regions of Galveston and Corpus Christi, Texas; Pensacola, Crystal River, and Miami, Florida; and Ocean Springs, Mississippi. Long-time mullet fishermen say they have seen the tumorous fish only in recent years, further suggesting a relationship to increasing pollution. Composition of the growths apparently differs among geographical regions. Those in Mississippi fit most, but not all, of the criteria of malignant cancers.

Most tumors on fishes are benign; that is, they do not grow fast, invade tissues, nor metastasize. The most common of these, a papilloma somewhat similar to a wart, occurs occasionally on a few fish, the black

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Figure 197. Large black drum with benign tumorous growth on chin. This papilloma, similar to a wart, rarely occurs on fish from the northern Gulf. This fish from a public aquarium developed the growth while in a large display tank.

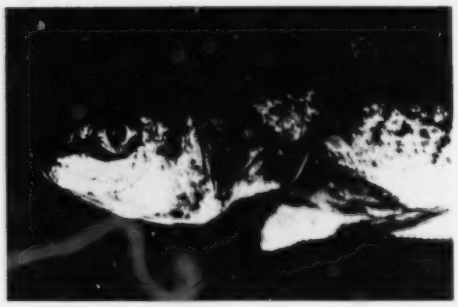

Figure 198. A rubber band girdling an Atlantic croaker. Tissue has grown around the hole in the dorsum and separated some of the fish's tissue ventrally.

drum being an example (Figure 197). The drum acquired the growth of a long-time resident displayed in a public aquarium.

Anomalies also result from injuries. Examples of wounds have already been presented. Chitinoclastic (chitin-attacking) bacteria essentially tattoo wounds on crustaceans. Fishes on occasion lose their tails or other helpful but nonessential structures. Many of these fish survive, if sheltered from predators. One local example of wounding concerns an Atlantic croaker which caught itself in a rubber band. After a period of time the fish apparently grew around the band, leaving the band to perforate and disfigure its body (Figure 198). Unfortunately, plastic beer can holders, rubber condoms, and other items slow to degrade may cripple many fishes. A packing strap around a shark has already been illustrated (Figures 186 and 187).

A reader should also realize that plastic bags, even though they may mess up a boat, do a lot of damage to the intestinal tract of a sea turtle or other animal that normally feeds on jellyfish and other such items resembling the bags. If someone is bent on throwing garbage in the water, a can might be the easiest to rationalize. Most cans provide shelter for small gobies and blennies which in turn harbor some harmless parasites which most certainly should be perpetuated.

TECHNICAL ASPECTS

SYMBIOSIS

Textbooks on parasitology are beginning to treat many host-parasite associations more generally as symbiotic ones. The variability in the amount of dependency of a particular symbiont on its host under different conditions makes a more generalized symbiotic approach the most practical one. Texts treating a variety of types of symbiotic relationships include those by Henry (1966;1967), Read (1970), Noble and Noble (1971), Cheng (1973), and Schmidt and Roberts (1977). Few texts of any sort emphasize marine relationships. Those that do usually stress diseases (*e.g.*, Sindermann, 1970).

Dales (1957) presented a review of some commensal relationships, listing numerous hydroids and anemones with their partners. Several additional uncited associations exist in the Gulf.

The example of *Clytia* sp. on *Donax roemeri protracta* and other species of *Donax* noted above points out problems in assigning a specific form of symbiosis, in this case phoresis, to any particular symbiotic couple. A strict definition of phoresis demands that neither party be physiologically dependent on the other. The hydroid may depend on the clam. It rarely infests any other substratum. Richard Heard has found it on old large specimens of the mole crab *Emertia talpoida* in Georgetown, South Carolina, but why does

it not attach to other hard items along high energy sandy beaches? Maybe it does. If so, maybe when it does, the item washes ashore or becomes otherwise unable to support the hydroid or the hydroid's character changes such that biologists consider it a different species. Loesch (1957) reported an absence of digenean parasites in clams with the hydroid or an attached alga. Tiffany (1968), however, did not obtain similar results. He found coquina over 25 mm long all had digeneans, whether commensals were present or not. Actually, Loesch encountered few infected clams, and the suggested loose form of mutualism based on the hydroid's preventing parasitic infections is doubtful.

In an unpublished study, Joyce (1961) suggested that the hydroid *Podocoryne carnea* (actually *Podocoryne selena*, see Mills, 1976) in Cedar Key, Florida, required a living snail shell, whereas *Hydractinia echinata* "preferred" a shell occupied by a hermit crab. Matthews and Wright (1970), Defenbaugh and Hopkins (1973), and Mercando (1976) provided additional observations. All three works reported a tendency for hydroids to live on shells occupied by *Pagurus longicarpus* and *Pagurus pollicaris*, but not other hermit crabs. The first authors noted that colonies of *Hydractinia echinata* were usually moribund when on shells occupied by the crab *Clibanarius vittatus*. When deprived of a shell, 80% of the specimens of *Clibanarius vittatus* refused a shell covered with that hydroid, and those that accepted the shell removed the polyps before entering it. Apparently *Clibanarius vittatus* is more sensitive to stinging than species of *Pagurus*, and those pagurids have an advantage over the more abundant *Clibanarius vittatus* when there is a fight over possession of a shell. Laboratory experiments could shed some light on this intriguing problem!

Anyone interested in the anemone-crab relationship will find that several such relationships have been examined. Indeed, Ross (1974) gathered together most of the information known on the behavior, physiology, ecology, and zoogeography of the partners and used that information to formulate ideas on the evolution of the associations. He (e.g., 1967) has presented other reviews on the behavioral aspects of the relationships.

The terms "zooxanthellae" and "zoochlorellae" have no taxonomic significance when applied to invertebrate-algal relationships. The names refer to the green or brown colored algae just as "cyanellae" refers to a blue-green colored mutualist. Actually dinoflagellates, cryptomonads, diatoms, blue-green algae, red algae, and other algae have been reported as symbionts. Henry (1966) presented many examples. The inability to culture most algal species and to extract them from living hosts has affected the understanding of associations. Smith (1973) presented a brief review of algal associations, drawing mostly from the examples of corals and their zooxanthellae, hydra and its chlorella, molluscs and their chloroplasts, and a small platyhelminth and its alga, a normal component of the adjacent phytoplankton. In the case of the flatworm, other related algal species can be established in it, but if the normal symbiont is then exposed to it, the worm ejects the alien alga and acquires the usual one. The symbiotic interaction involves more than nutritional processes! Taylor (1974) discussed the taxonomy of all described symbiotic marine algae and presented information on their biology. A very useful paper, it will help anyone initiating a study on algal symbionts.

In the two species of *Zoanthus* from Florida, I found the typical golden-brown vegetative stage of a dinoflagellate resembling those of the genus *Gymnodinium* or *Exuviaella* (probably *Gymnodinium microadriaticum*) within the gastrodermis. Embedded in the epidermal tissue occurred bacteria, diatoms, and what may be another algal symbiont which did not fluoresce light. However, the presence of chlorophyll a, as determined with a Beckman DK-2 spectrophotometer, was confirmed in tissue stripped of diatoms. Internally, a few species of colorless flagellates resided. One large flagellate extended over 40 μ in length not including the flagellum, and another stored considerable starch. Even the vegetative stage of the dinoflagellate occurred in a flagellated motile carrier cell.

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A method of observing objects with chlorophyll is to use fluorescent microscopy. I found the dinoflagellate to fluoresce red, and, under a squash preparation, a few individuals showed dividing stages. Fluorescent microscopy also revealed elongated homogeneous boat-shaped objects that differed some between the two zoanthids. Instead of being red like that of most chlorophyll, the fluorescence was a chartreuse green similar to that produced by members of *Peridinium*, dinoflagellates that possess armor in their motile stage. This material appeared to be packaged from granular material in mesogleal cells and was transported throughout the organism. Its function is unknown.

Considerable work has already been conducted on zoanthid feeding. Trench (1974) provided an extensive study on the photosynthetic contribution of the intracellular *Gymnodinium* species and how it passes that material on to "*Zoanthus sociatus*." Ultimately the algal cells apparently undergo senesence, but still are not digested by the host.

Food other than the photosynthate from the alga also is utilized. Digestion occurs intracellularly after cells engulf small particles. Sebens (1977) assumed that the zoanthid studied by Trench was actually *Zoanthus solandri*. The taxonomy remains to be clarified. In any event, what Sebens considered *Zoanthus sociatus* feeds on smaller items than *Zoanthus solandri*. These include small crustaceans, foraminifera, and apparently detritus. When not provided this external source of food, both mentioned species lost weight. Some other zoanthids tested by Sebens did not lose weight, suggesting that they, unlike the two species of *Zoanthus*, derived all their energetic needs from their algal symbionts. Reimer (1971) also studied different feeding behaviors of zoanthids, but she used Pacific species.

Other than Trench (1974) who reported aggregates of unidentified bacteria on the cuticle, no other authors to my knowledge have reported more than the single dinoflagellate symbiont in a host. The identification, function, and interaction of other symbionts needs investigation. Perhaps these organisms are vital to the life of a zoanthid, and perhaps their presence or abundance varies according to locality or season.

This knowledge would provide a remarkable understanding of a very complex "simple animal." Even with the help of E.J.F. Wood and John F. Kimball, I was unable to culture any of the internal symbionts using several modifications of methods used by McLaughlin and Zahl (1957) and Provasoli, McLaughlin, and Droop (1957). Perhaps someone using more modern techniques and approaches can succeed in this task.

THE AMERICAN OYSTER

The American oyster, *Crassostrea virginica*, acts as a host or substratum for a large number of symbionts. The "bible" on all aspects of the oyster (Galtsoff, 1964) presents considerable information on most of these. Cheng (1967), Sindermann and Rosenfield (1967), and Sprague (1970b) provide more recent compilations on symbionts from molluscs in general. Other pertinent reports dealing with *Crassostrea virginica* include those by Sprague (1971) and Sindermann (1977). MacKenzie (1977) discussed some oyster symbionts in conjunction with an appraisal of the oyster fishery and an aquacultural program to rehabilitate damaged reefs in Mississippi. Citations referring to work on specific organisms occur in all the above articles and others are cited below. Several infectious and noninfectious diseases that involve oysters from the Gulf have not been treated here.

Parasites of another oyster, the smaller Gulf oyster (*Ostrea equestris*), have not been reported as extensively. This oyster occurs in high salinity regions, has rows of small "teeth" bordering the inner margins of the valves, and lacks pigmentation on the adductor muscle scar.

Overstreet and Howse (1977) provided a brief review of the public health aspects of eating raw oysters and of coming into contact with polluted waters in Mississippi. Unquestionably, the most dreaded disease

from eating raw oysters locally is hepatitis, but others, primarily bacterial and viral, also can be contracted. A few other types of microorganisms may also have potential public health significance (Harshbarger, Chang, and Otto, 1977).

Much of the ecological information about *Dermocystidium marinum* came from a study by Quick and Mackin (1971) in Florida. Other extensive investigations have been made by Ray (1954), Andrews and Hewatt (1957), and Mackin (1962). For those interested in classification of the organism, the species has been transferred from *Dermocystidium* and was known as *Labyrinthomyxa marina* for several years. After some uncertainty, Perkins (1976a; 1976b), using ultrastructural evidence, considered it a coccidian or related protozoan, and Levine (1978) has now established it as a protozoan named *Perkinsus marinus* after Perkins.

Several other species exist in oysters and other molluscs; Quick (Dow Chemical Company, Freeport, Texas, personal communication) estimates at least four or five *Labyrinthomyxa*-like organisms affect the oyster alone. Most of these usually occur in low numbers and do not harm the oyster unless it experiences other stresses. Upon culturing with thioglycollate and other media, these organisms respond in a variety of different ways and morphological types. Often more than one species will infect the same individual oyster. Much more effort should be given to understanding these organisms and their relationships with their invertebrate hosts and their environments. In fact, *Labyrinthomyxa patuxent*, first described in 1921, a potentially-lethal pathogen, and the focus of considerable research (Mackin and Schlicht, 1976), may be related to what many authors consider neoplastic (tumor) diseases of molluscs. Whether that organism, with its incomplete response to thioglycollate medium, occurs in the Gulf has not been firmly established. The method for the improved culture medium has been documented and discussed by Quick (1972).

A disease not discussed above because it apparently does not affect oysters in the Gulf is "MSX" (for Multinucleate Sphere X). Losses as high as 85% of planted oysters from some regions along the northeastern U.S. coast have been attributed to this disease, now known to be caused by the haplosporidan *Minchinia nelsoni* based on evidence by Couch, Farley, and Rosenfield (1966). Both it and *Minchinia costalis* cause disease and have attracted considerable attention concerning their morphology (Perkins, 1968; 1969), reduced reproductive capacity of infected oysters (Couch and Rosenfield, 1968), and mortalities caused by the two haplosporidans (Andrews, Wood, and Hoese, 1962; Farley, 1975; Kern, 1976). Even though most oysters in a reef may be killed, survivors and their progeny appear to develop a resistance. Consequently, either transplanting uninfected oysters into an enzootic region or introducing an infected oyster into a region free of the haplosporidan disease can have short-term devastating effects!

Apparently more than two species of sporozoan gregarines infect the oyster. Spores of *Nematopsis ostrearum* lodge primarily in the mantle, and those of *Nematopsis prytherchi* and perhaps another undescribed species primarily involve the gills. Quick (1971) encountered unidentifiable spores near the digestive tissues of oysters from central but not northern Florida. Decapod hosts for *Nematopsis ostrearum* include several mud crabs, whereas the host for spores in the gills is the stone crab. Mackin (1962: 203-205) questioned whether any of these species causes oyster-mortalities as suggested by several authors. *Nematopsis* spores, generally larger than those of *Dermocystidium marinum*, can be seen in histological sections or in fresh tissue partially digested for about a minute in a few drops of 10% sodium or potassium hydroxide solution.

Nematopsis ostrearum appears to be involved in a dynamic equilibrium in oysters from Virginia (Feng, 1958). That is, when oysters heavily or lightly infected get transplanted to other regions with oysters having light and heavy infections, respectively, the transplants alter the intensity to assume average levels for the region. Such ideas should be investigated

further using oysters in the Gulf.

At least two species of *Stylochus* plus other polyclads occur in oyster beds of Mississippi (Hyman, 1940). *Stylochus ellipticus*, a cream to brownish worm reaching about 25 mm long, is much more prevalent than the grayish 50 mm long *Stylochus frontalis*. The latter, much more common in Florida, was studied by Pearse and Wharton (1938), who presented ecological and biological data on it as the synonym *Stylochus inimicus* as well as some data on *Stylochus ellipticus* under the name *Eustylochus meridianalis*. The latter withstands water of lower salinity and temperature than *Stylochus frontalis* and is less specific toward oysters. Both species lay single layers of egg-masses on oyster shells or other hard surfaces.

The oyster crab rarely occurs in most Gulf regions, but because students often wonder about problems they could undertake, I think it worthwhile to mention here that several species of small pinnotherid and porcellanid crabs associate with a variety of invertebrates and provide an easily visible animal to study. If a person collects penshells or scallops, digs up burrows of mud shrimps (callianassids), or investigates the tubes or burrows of polychaetes, holothurians, or sipunculids, he will probably encounter several species of pea crabs. They can probably be identified using the keys by Williams (1965) or Felder (1973).

Many questions concerning each different pea crab could be asked. Are young produced over long periods? Does the first stage crab always invade the host? Are young individuals chemically attracted to hosts? What is the dependency and pathological effect of the crab on the host? What is the longevity of both sexes? Will additional females enter an already occupied habitat? When several females associate with a host, will some migrate to nonassociated hosts when they change into a hard stage? Can the crabs survive harsher conditions than their hosts? Do attached hydroids aid the crabs? A place to initiate a literature search for any such investigation could be articles by Christensen and McDermott (1958), Haven (1959), Davenport, Camougis, and Hickok (1960), and Sastry and Menzel (1962).

The small pyramidellid gastropod along the edge of an oyster shell can be identified using Abbott's (1974) book. Hopkins (1956c) and Allen (1958) both discussed the *Odostomia impressa*-oyster relationship.

Oyster growth shows a relationship with bucephalid infections (Menzel and Hopkins, 1955), although more extensive studies are needed.

The pathogenic effect by normally commensal inhabitants to stressed oysters has not been well documented in most cases. Stress from high temperatures apparently causes dermo to harm the host. Other examples also exist. Ciliates occasionally infect a healthy oyster, but may become a complicating factor in weakened hosts as a secondary invader (Mackin, 1962; Pauley, Chew, and Sparks, 1967). The latter workers observed a ciliate to infect heavily the Pacific oyster after they injected turpentine, but not a nonirritant, in the adductor muscle or in connective tissue.

Even though burrowing organisms affect oysters and other molluscs, few studies have treated them in detail. Alfred Chestnut at GCRL provided most of the information on the oyster burrowing clam, or martesia (*Diplothyra smithii*), used here. His dissertation will present details of the biology of this intriguing clam. The mud worm *Polydora websteri* can be easily identified using Blake's (1971) key. Another species, *Polydora ligni*, also occurs in oyster reefs, but forms fragile tubes of silt rather than burrowing in shells. It, however, can reproduce rapidly and smother the oysters. Hartman (1958) presented a taxonomic treatment on the several species of burrowing sponges, and Wells, Wells, and Gray (1960) added sizes of perforations in the shell in addition to other characteristics. Hopkins (1956a; 1956b) reported ecological data on the different species. He considered the presence of *Cliona celata* to indicate that salinity remained below 10 ppt about one fourth of the time and that of *Cliona truitti*, a species favoring high salinity, to indicate that the salinity seldom dropped below 15 ppt. For those interested in animal-burrowing, an entire issue of *American Zoologist* (Carriker, Smith, and Wilce, 1969) provided many specific and general articles

treating the subject.

The section on predation by Galtsoff (1964) can be amplified by reading the interesting findings of McDermott (1960) who studied predation of oysters by mud crabs. Kay McGraw has been investigating predation by the blue crab in her doctoral work on growth and survival of hatchery-reared oysters. McGraw and Gunter (1972) investigated predation by the drill in Mississippi. Larval development of this most important predator, *Thais haemastoma*, was described by D'Asaro (1966).

THE BLUE CRAB

The blue crab fishery in Mississippi has been discussed by Perry (1975). Others have treated it in adjacent regions in the Gulf (e.g., Darnell, 1959; More, 1969; Jaworski, 1972; and Adkins, 1972). Tagatz and Hall (1971) presented an annotated bibliography on *Callinectes sapidus*. Pyle and Cronin (1950) described its anatomy. Phyllis Johnson is finishing a histological study, and Overstreet and Cook (1972) discussed soft-shelled crabs and their potential for further exploitation.

So far I have not said anything about the lesser blue crab, *Callinectes similis*, or, as some fishermen call it, the Gulf or scissor bill crab. It also occurs in the northern Gulf and the eastern U.S. seaboard (Williams, 1974) and helps make up a part of the blue crab fishery. It, however, does not reach the size of *Callinectes sapidus* and can be further separated from it by possessing two large and two small "teeth" projecting along the front of the carapace between the eyes rather than just two large ones. This count does not include the projections where the eyestalks protrude. Also, small specimens of *Callinectes similis* have a blue patch at the "elbow" and where the claw articulates, rather than being red like on *Callinectes sapidus*.

The parasites infecting the two crab species also differ in some cases. A critical study of all the parasites of the two has not been made, even though numerous papers cover individual species infecting *Callinectes sapidus*. As far as I know, neither *Ameson michaelis* nor *Loxothylacus texanus*, both internal parasites, infect *Callinectes similis*. I tried to infect a few individuals with the microsporidan without success. On the other hand, I have seen a nonencysted larval cestode plerocercoid extensively invading the skeletal muscles of the lesser blue crab (Figures 26 and 27), but have never seen it in the regular blue crab. On the basis of examining muscle tissue from numerous specimens of *Callinectes sapidus*, both Phyllis Johnson and Richard Heard (personal communication) have each seen but a single specimen of a larval cestode. Heard's specimen was encountered in the Florida Keys. Most external symbionts infest both crabs, and their presence depends on ecological variables. The remaining discussion relates entirely to infections in *Callinectes sapidus*.

The first of four viruses infecting eastern blue crabs, according to Phyllis Johnson (1977b), is a reolike virus found in hemopoietic tissues, hemocytes, glia of the central nervous system, and other cells. If infected hemolymph is injected into the body cavity of a crab, the crab may die within 3 days, probably from neurological involvement, compared to 12 to 32 days for crabs fed injected tissue. The second is a herpeslike virus mainly in hemocytes (Figures 44 and 45) which takes about a month to kill a confined crab and perhaps much longer to kill or severely affect an unstressed host in its natural environment. Crabs do not appear distressed until near death, at which time their hemolymph turns chalky white. The third is a picornalike virus infecting primarily neurosecretory cells, epidermis, and bladder epithelium and secondarily invading blood cells and other tissues. After about a month, the crab, affected by an altered molting pattern and sometimes by blindness, may die. The fourth is a baculovirus infecting the hepatopancreas that does not appear to cause overt disease. Most of these and other viruses probably affect the blue crab in the Gulf. Infections to date have been confirmed solely on the basis of ultrastructural examination of specimens from the Atlantic seaboard (P. Johnson, 1977b).

A variety of chitinoclastic bacteria have

been isolated from crabs and shrimp in Mississippi (Cook and Lofton, 1973). One strain, *Beneckea* type I, was isolated from all necrotic lesions, making it suspect as a primary causative agent that invades wounded hosts. Shell disease in the blue crab, caused by one or more opportunistic organisms, has only been reported relatively recently (Rosen, 1967; Sandifer and Eldridge, 1974), but has long been considered a problem to crabbers who maintain crabs in floating cypress cages or who leave crabs in traps for extended periods. Overstreet and Howse (1977) discussed the need to investigate the relationship between stress and causative agents.

Crabs collected by trapping, trawling, or dredging typically have systemic bacterial infections which are undetectable other than by culturing the bacteria. Many such crabs with bacteria in their hemolymph appear to be, and probably are, relatively healthy (Colwell, Wicks, and Tubiash, 1975; Sizemore, Colwell, Tubiash, and Lovelace, 1975). Most of these bacteremias are probably transient, and some may be misdiagnoses based on cultures of contaminants from the cuticle. Disease typically ensues only when the organism is especially virulent or when the host is stressed. Heavy infections can kill crabs (*e.g.*, P. Johnson, 1976). Overstreet and Howse (1977) report mortalities of crabs in traps caused by *Vibrio parahaemolyticus*.

Vibrio parahaemolyticus, a gram negative, rod-shaped, motile bacterium has also been implicated in human disease. Many strains live and multiply rapidly in marine waters, especially at the human body temperature of 37°C. In contrast, most strictly human pathogens cannot reproduce in seawater. These organisms concentrate in marine organisms near sewage outfalls and give most raw seafood products an undeserved poor reputation. Just like several other bacteria though, *Vibrio parahaemolyticus* usually produces symptoms of nausea, diarrhea, vomiting, and mild fever. It has also been implicated in infections of the skin. Lee (1973) discussed information that seafood processors should know about the organism.

Most of the microsporidans infecting the blue crab as well as other hosts have been treated by Sprague (Bulla and Cheng, 1977). I am presently working on another species. Sprague recently changed the name of the most prevalent species, *Ameson michaelis*, when he transferred it from the genus *Nosema*. Some aspects of its development have been described by Weidner (1970; 1972). Overstreet and Weidner (1974) suggested that the muscle disintegration induced by *Ameson michaelis* may be more severe and extensive than that caused by several other microsporidans because the spores of this species lack a surrounding pansporoblast. A growth chamber bounded by one or more membranes, the pansporoblast may trap potentially harmful metabolites.

If in the future the crab industry rears its product for the soft-shelled crab market, means to prevent and control infections of microsporidans will be necessary. Steps in these directions have already been made (Overstreet, 1975; Overstreet and Whatley, 1975; Sindermann, 1977).

A helpful listing of many protozoans from decapods was presented by Sprague and Couch (1971). Many other papers treat different aspects of infections and their causative agents in detail, and a few of these will be mentioned. P. Johnson (1977a) critically investigated paramoebiasis; the agent has been adequately described by Sprague, Beckett, and Sawyer (1969) and by Perkins and Castagna (1971). Newman and C. Johnson (1975) reported the dinoflagellate *Hematodinium* sp., and Couch (personal communication) has additional studies in progress. Newman, Johnson, and Pauley (1976) described the *Minchinia*-like haplosporidan. Three papers (Couch, 1966; 1967; 1973) treated the ciliate *Lagenophrys callinectes*, and Overstreet and Whatley (1975) reported the internal "holotrich."

Bland and Amerson (1973a; 1973b) reported the fungus *Lagenidium callinectes* from crustacean ova, and continuing work by Bland's group has developed control measures (Bland, Ruch, Salser, and Lightner, 1976).

In a dissertation on microphallid digeneans of fiddler crabs, Richard Heard (1976) additionally treated some species from the blue crab and from other

crustaceans. He corrected and added data to the earlier reports on *Microphallus basodactylophallus* (= *Carneophallus basodactylophallus*) by Heard (1967) and Bridgman (1969). Even considering the nomenclatural treatment of the species in a monograph by Deblock (1971), problems still exist, as pointed out by Heard. Heard also elucidated additional aspects of the life cycle of *Levinseniella capitanea*, a worm described by Overstreet and Perry (1972). The cycle progresses much the same as *Microphallus basodactylophallus*; however, fewer mammals and birds probably host the worm than for many microphallids, since I could not establish specimens in mice, rats, or baby chicks.

Many microphallid metacercariae, including those discussed, produce eggs when maintained in warm saline. This ability reflects the lack of much biochemical dependency on the host for egg production in those microphallids. The important aspect of the life cycles of those species seems to be the need for adults to produce eggs quickly, a maneuver allowing infection of intermediate hosts if the definitive host is one that would soon migrate from the region and thereby leave potential intermediate hosts behind.

Various histological studies treating the hyperparasite *Urosporidium crescens* from the Atlantic coast list digeneans of the blue crab other than *Microphallus basodactylophallus* as probable hosts (De Turk, 1940; Sprague, 1970a; Perkins, 1971; Couch, 1974a); however, Heard and I have examined specimens of trematodes from infected crabs from Virginia and found them to be *Microphallus basodactylophallus*, the same as in the Gulf. On the other hand, additional digeneans are suitable hosts for this haplosporidan including *Microphallus choanophallus* and *Levinseniella capitanea*.

The acorn barnacle, *Chelonibia patula*, and the pedunculate barnacle, *Octolasmis muelleri*, have been reared in the laboratory by Lang (1976a; 1976b). Those works suggest that distribution of both species depends on temperature. Breeding and larval development ceases below about 15°C. Development from the first naupliar to cyprid stage of *Octolasmis muelleri* takes about 2 to 3 weeks at 24 to 27°C and less for the other barnacle. Development to that cyprid stage, the stage which attaches to the host, prolongs considerably in cooler water. Diet also controls development, and the pedunculate barnacle necessitates a much more specific diet. Observations on that species from North Carolina were documented long ago (Coker, 1902). However, whether or not specimens from the blue crab in America comprise a geographic population and a synonym of the cosmopolitan *Octolasmis lowei* has not been established decisively (*e.g.*, Newman, 1967).

Ecological studies of *Loxothylacus texanus* in the northern Gulf were presented in some detail by Ragan and Matherne (1974) who additionally cited most of the references on that species in their bibliography. The only other reported host in addition to *Callinectes sapidus* is *Callinectes ornatus*. Gordon Gunter has seen that crab infected along the west coast of Florida (Christmas, 1969), and I have seen many in the shallow hot regions of Bear Cut in Miami, Florida. Lawler and Shepard (1978) present a fairly complete bibliography on all rhizocephalans. From Mississippi, Christmas (1969) reported infected blue crabs and also mentioned the presence of what he tentatively considered *Loxothylacus panopaei* in mud crabs.

Loxothylacus panopaei is an important example of introduced species. After many oysters in Chesapeake Bay died from *Minchinia nelsoni*, oysters from the Gulf of Mexico were introduced in 1963 and 1964 to help reestablish the population. Incidental to the oysters occurred mud crabs infected with the rhizocephalan. By 1965, native mud crab populations started revealing infections of *Loxothylacus panopaei* for the first time (see Van Engel, Dillon, Zwerner, and Eldridge, 1966; Daugherty, 1969). Couch (personal communication) has also found *Eurypanopeus depressus* infected in Chincoteague Bay (Figure 36).

Soon after first being introduced, a successful species often produces excessively large populations until such time that an equilibrium becomes established. Whether

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infections of *Loxothylacus panopaei* spread explosively has not been established, but the apparent abundance of mud crabs declined. Possibly the parasite did not influence the population structure of the crabs, but, nevertheless, introductions of one species may result ultimately in a decline in other species in the new habitat. Before introducing any animal or plant, the need for it and the possible side-effects from the introduction should be carefully evaluated.

Humes (1942) presented an extensive treatment on the nemertean *Carcinonemertes carcinophila*, which was later followed by a paper on its use as an indicator of host spawning (Hopkins, 1947) and another on its larva (Davis, 1965).

The fact that the common leech *Myzobdella lugubris* uses a fish to obtain blood and a crab on which to deposit cocoons has been recognized only recently (Daniels and Sawyer, 1975; Sawyer, Lawler, and Overstreet, 1975). The latter reference goes into considerable detail on salinity-tolerances of the adult and developing leech. Hutton and Sogandares-Bernal (1959) reported the association between the leech and crab mortality. Some data on the branchiobdellid *Cambrincola mesochoreus* were reported in an unpublished honor's thesis by Blackford (1966), but more extensive work could be done on that and other branchiobdellids of both the crab and crayfishes in the northern Gulf region. The authority on that group is Perry C. Holt at Virginia Polytechnic Institute and State University.

PENAEID SHRIMPS

Considerable data have been published on shrimp catches and shrimp biology. Pérez Farfante (1969) provided a detailed taxonomic and ecological treatment and a review of all members of the genus *Penaeus* in the Western Atlantic. Of the two common species in the northern Gulf, the brown shrimp has a groove (lateral rostral sulcus) running along each side of the dorsal (top) midline ridge on the "head" (cephalothorax) as well as one on the last (sixth) abdominal (tail) segment. The white shrimp lacks these, but not the pink shrimp, which may additionally have a distinguishing brownish lateral spot on the second and third segments. Cook and Lindner (1970) and Lindner and Cook (1970) presented good summaries of data on the brown and white shrimps to which could be added a paper on burrowing and daily activity of shrimp by Wickham and Minkler (1975). Christmas and Etzold (1977) edited a report on a regional fishery management plan for penaeid shrimp.

The parasites and diseases of commercial penaeids, more than those of most any other select group of marine organisms, have been studied in some detail. A considerable number of questions remain unanswered, but recent findings and summaries of previous works have been presented by Overstreet (1973), Feigenbaum (1975), S. Johnson (1974; 1975), Lightner (1975), and Couch (1978). Couch broadened his paper further by including the response of shrimp and their tissues to a variety of toxic chemicals and heavy metals. The observations on the tumorous growth, a hamartoma, discussed above were made by Overstreet and Van Devender (1978).

Couch (1974b) first observed the viral inclusion bodies in shrimp and followed his report with a series of studies assessing the relationship between stress and disease (Couch, 1974c; see citations by Couch and Courtney, 1977). The virus was characterized by Summers (1977). Flagellate and ciliate protozoans additionally involved some of the dying larval shrimp, but no doubt exists about the increased presence of the inclusion bodies in shrimp experiencing certain stresses.

The normal bacterial flora of brown and white shrimps was investigated by Vanderzant, Mroz, and Nickelson (1970). Lightner (1975), who reported the epizootic of virulent chitinoclastic bacteria, reviewed bacterial diseases of shrimp in general.

Research on fungal diseases of crustaceans has just begun to receive serious investigation. Unestam (1973), Bland (1975), and Lightner (1975) provided good summaries of the problems.

"Black gill disease" results from a variety of both infectious and noninfectious agents. Massive accumulations of hemocytes settle within the gill filaments, ultimately associated with dysfunction, destruction, or secondary infections. Lightner and Redman (1977) showed histologically that the inflammatory responses typically involve melanin deposition following exposure of shrimps to cadmium, copper, and *Fusarium solani*, as well as when shrimp have an ascorbic acid deficiency, wounds, and a variety of undiagnosed conditions. Inflammatory response in penaeid shrimp involves fixed phagocytes lining blood sinuses, phagocytes in loose connective tissue, fibrocytes, and three forms of hemocytes. Solangi and Lightner (1976) followed the response to the fungus, Fontaine and Lightner (1975) described the encapsulation, phagocytosis, and elimination of necrotic material as well as the healing process, Couch (1977) presented an ultrastructural study of lesions in gills exposed to cadmium, and Sindermann (1971) reviewed the internal defenses of crustaceans in general.

The four common microsporidans differ in several aspects (Overstreet, 1973) and will be described because of the difficulty in distinquishing them and because of their receiving a recent resurgence of interest. Spores of *Ameson (= Nosema) nelsoni* measure about 2.5 μ long by 1.5 μ wide (occasionally up to 3.5 μ by 2.3 μ) with a narrow polar filament 23 μ long. The single spore has no pansporoblast chamber, and masses of them surround the abdominal muscle bundles of white, brown, and pink shrimps before eventually replacing them. *Pleistophora* sp. may be especially difficult to distinguish from the above species. Chromatophores along the dorsolateral surfaces of shrimp infected with both species expand and produce a bluish-black appearance to the shrimp; however, the appearance usually is darker when the shrimp is infected by *Pleistophora* sp. Spores of that species, 1.7 to 3.0 μ long by 0.9 to 2.5 μ wide with polar filaments 42 to 125 μ long, develop in pansporoblasts containing as few as 14 spores or as many as several hundred. The *Pleistophora* sp. infections typically replace muscle tissue and sometimes invade anteriorly-located tissues in addition to the tail; they involve primarily white and brown shrimps. The third species from the host tail, *Thelohania duorara*, lies between muscle fibers, most commonly in pink shrimps. As with *Pleistophora* sp., it occasionally invades heart and other tissues. Spores measure 4.7 to 6.8 μ long by 3.0 to 4.2 μ wide (averaging 6.0 by 3.7 μ) with uniformly wide polar filaments 97 to 142 μ long; eight of them exist within each pansporoblast.

The last species (*Agmasoma [= Thelohania] penaei*) invades tissue other than the abdominal muscle. Prevalent in blood vessels, foregut, and hindgut, it also infects and destroys the germinal tissue of the gonads. Infections seen through the carapace among the branchiostegal epithelium and in the appendages originate from tissue of the blood vessels. Only in an abnormal situation have I observed an infection associated with abdominal muscles (Overstreet, 1973). A pansporoblast harbors a group of eight pyriform spores either 2.5 to 4.7 μ long by 2.0 to 3.5 μ wide or 5.5 to 8.2 μ by 3.5 to 4.2 μ. Both the small and large (megaspores) spores occur in the same shrimp. Also, the polar filaments protrude 65 to 87 μ and have a thin distal portion contrasting with the thick proximal part. Other than some pond-reared pink and brown shrimp, only white shrimp have revealed infections. Iversen and Kelly (1976) apparently transmitted this or a related species to postlarval pink shrimp by feeding them feces from spotted seatrout that had eaten infected shrimp.

Descriptions of the different North American gregarines of penaeids occur in works by Sprague (1954), Kruse (1966a; 1966b), Overstreet (1973), and Feigenbaum (1975). Kruse (1966a; 1966b) provided information on the biology of a few species, and Sprague (1970a) reviewed gregarines of crustaceans in general.

Descriptive data on most ciliates are lacking. Couch (1978) gave a recent summary of most ciliate and flagellate species from shrimp, and papers by S. Johnson (1974) and by Lightner (1975) provided additional information. The

relationship between *Zoothamnium* sp. and the shrimp's gill has been studied by Foster, Sarphie, and Hawkins (in press), and the possible detrimental effects caused by that relationship were discussed by Overstreet (1973).

Heard experimentally infected the shrimp shown in Figure 68 and plans to report the results soon. Overstreet (1973) summarized information on the other trematodes, including a description of *Opecoeloides fimbriatus* by Kruse (1959).

Most of the common helminths have been reported by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), Kruse (1959), Overstreet (1973), Feigenbaum (1975), and Couch (1978). Feigenbaum (1975) discovered two new trypanorhynch cestodes from the hepatopancreas and body cavity of *Penaeus brasiliensis* near Miami, Florida, and Corkern (1978) found an encysted cyclophyllidean larva in shrimps in Texas. No one has seriously tried to determine the identity of the intestinal larval cestode. However, Tom Mattis has completed much of a dissertation problem at the Gulf Coast Research Laboratory on the life history of *Prochristianella hispida*. Figure 70 illustrates his present understanding of its cycle. Prevalence of that species, previously referred to as *Prochristianella penaei* (see Campbell and Carvajal, 1975), has been treated by several authors (Aldrich, 1965; Corkern, 1970; Ragan and Aldrich, 1972; Overstreet, 1973), and Corkern (1970) also included data on *Parachristianella dimegacantha*, a species common in younger shrimp from Galveston Bay, Texas.

In white shrimp studied by Sparks and Fontaine (1973), larval *Prochristianella hispida* developed a dense cyst in the hepatopancreas that was apparently soon destroyed and resorbed by the host. When in the hemocoel, the larva had a thinner cyst with less inflammatory response, suggesting a more preferable site. Those authors believed that worms are gradually lost in white shrimp. Because infections in brown shrimp do not reveal a decrease in intensity with age as assumed for those in white shrimp from some areas, the authors suggested brown shrimp may respond to infections differently. When shrimp can be readily infected, these hypotheses can be tested. Overstreet (1973) did not detect a decreased intensity of infections over the 2 to 3 month period shrimp were reared in Louisiana ponds.

Most investigators previous to or unaware of a study by Mudry and Dailey (1971) assumed shrimp acquired infections from small infected crustacean intermediate hosts. That study suggested that in cycles using a crustacean and elasmobranch, the crustacean acquired its infection directly by feeding on worm's eggs, whereas in cycles with a plerocercoid in a fish, the fish acquired the infection from a crustacean. The first method may not be representative for penaeid shrimp with *Prochristianella hispida*.

The larval ascaridoid from shrimp described by Kruse (1959), Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and others as *Contracaecum* sp. can presently be considered *Thynnascaris* type MA. Norris and Overstreet (1976) briefly discussed it and differentiated it from type MB. Type MB is 1 to 3 mm long with an esophagus 4 to 13% of that length, a ventricular appendage 14 to 68 times the length of the short intestinal caecum, and a spineless, bluntly-rounded tail. In contrast, type MA is 3 to 5 mm long, has an esophagus 14 to 15% of that length, has a ventricular appendage 2 to 3 times as long as the intestinal caecum, and possesses a spiny projection on the tail. Norris and Overstreet recognized three or four forms from penaeids.

Adult *Thynnascaris* species infect a variety of fishes. Norris and Overstreet (1975) described two adult forms and Thomas Deardorff of GCRL hopes to be able to correlate the adults of a few Gulf species with their larval forms by experimentally completing portions of their life cycles.

Spirocamallanus cricotus was first tentatively reported from penaeid shrimp as *Spirocamallanus pereirai* (see Overstreet, 1973). Fusco and Overstreet (1978), however, have now clearly established that the species

commonly referred to as *Spirocamallanus pereirai* from the Atlantic croaker and spot in the Gulf of Mexico constitutes a separate, closely-related species. Fusco (1978a) has described the larval stages of that worm.

Leptolaimus sp. (Leptolaimidae) from on the gills and from both within the lumen of and adjacent to the alimentary tract of brown and white shrimps was reported by Overstreet (1973).

Rigdon and Baxter (1970) first reported spontaneous necrosis of abdominal muscles of penaeids, and that work has been followed up by Lakshmi, Venkataramiah, and Howse (1978), who showed that the lesions, presumably caused by muscle fatigue heal faster in oxygenated rather than aerated water. The cramped condition was first reported by de Sylva (1954) and then subsequently by Johnson, Byron, Lara M., and Ferreira de Souza (1975). Venkataramiah, Lakshmi, and Biesiot at GCRL have found that cramping occurs most often in conditions of low salinity and temperature. They (personal communication) also determined that it results from an internal ionic imbalance, and they are presently trying to identify the specific ion or ions involved. Both necrosis and cramping typically affects shrimps in tanks for bait dealers and in culturing facilities. As culturing shrimp becomes more widespread, especially with heated or cooled water, these and other diseases will appear. One of these others is gas-bubble disease (Lightner, Salser, and Wheeler, 1974), and it also affects oysters and clams in water supersaturated with oxygen or nitrogen.

Overstreet (1973) discussed the golden shrimp disease and also reported and reviewed some fouling organisms. Many organisms foul shrimp, even a barnacle that settles on the blue crab (Dawson, 1957).

Just like different tissues of all animals, those of shrimp degenerate at different rates after death. Lightner (1973) described these postmortem changes in the brown shrimp at different temperatures.

GRASS SHRIMP

In addition to his illustrated handbook (1975) on shrimp diseases for those culturing shrimp, S. Johnson (1977) also provided a similar handbook on diseases of crayfish and freshwater shrimp. Although not complete for diseases of grass shrimp, that pamphlet provides the only single source of parasites of that host. It contains much useful information, some taken from an earlier paper (S. Johnson, 1974). Many of the protozoans symbiotic on the grass shrimp were listed by Sprague and Couch (1971). The findings of more species plus completion of considerable detailed biological studies on many protozoans of grass shrimp and other crustaceans have occurred since 1971. Clamp (1973) provided observations on *Lagenophrys lunatus*, and Phyllis Bradbury has worked up several other ciliate-grass shrimp relationships including that for *Terebrospira chattoni* (see Bradbury, Clamp, and Lyon, 1974; Bradbury and Goyal, 1976). Sprague (Bulla and Cheng, 1977) listed three microsporidans from *Palaemonetes pugio* and more information on those have been presented by Street and Sprague (1974) and Overstreet and Weidner (1974).

The bopyrid *Probopyrus pandalicola* has been studied by Richard Heard (unpublished). Also, its respiration in both larval and adult stages has been investigated in relation to its two hosts (Anderson, 1975a; 1975b). Both the infested copepod and shrimp respired less than their respective control counterparts. This decreased use of oxygen may result from a lipid buildup in infested hosts requiring less energy to metabolize. When fish have parasitic infections, they generally respire more, which in turn increases their stressed condition.

FISHES

A general treatment of the biology of fishes can be obtained from a multitude of books available in most any library. Identifications of most species from the northern Gulf of Mexico can be made using keys in a book by Hoese and Moore (1977). Walls (1975) also wrote a recent book on these fishes. A standardized list of common

and scientific names acceptable to the American Fisheries Society was published (Bailey *et al.*, 1970), and another edition will update it in the future. These are common names used in most scientific literature, and not necessarily those used in specific geographic localities by fishermen. Older works, such as an article by Earll (1887) used for comments on the early mullet fishery, often use scientific and common names no longer in use today.

Because of recent interest in elasmobranchs and the potential for investigating evolutionary aspects of some highly specific elasmobranch parasites, I mention a few references. A book edited by Gilbert, Mathewson, and Rall (1967) covered most aspects of elasmobranch biology except the parasites. More current evaluation of interrelationships among elasmobranch groups has been presented by Zangerl (1973) and Compagno (1973; 1977). Means for critical identification of species have been given by Bigelow and Schroeder (1948).

No single source covers parasites from marine or estuarine fishes. Hoffman (1967), however, covered parasites in North American freshwater species, and that book might be helpful for identifying some parasites. A rather extensive compilation of mullet parasites and diseases (Paperna and Overstreet, in press) may also apply to a general investigation of conditions in any fish. Control and treatment of freshwater diseases have been covered extensively (Hoffman and Meyer, 1974). Methods for diagnosing and controlling selected diseases in salmon, pompano, and striped bass have been edited by Sindermann (1977), but the same statements also apply to several other host-disease relationships.

Microbes

Plumb (1974) reviewed all known viral diseases of fishes from the Gulf region. Lymphocystis from Atlantic croaker was first described by Howse and Christmas (1970; 1971) and that from the silver perch by Lawler, Howse, and Cook (1974). A brief review of infections including some new data was presented by Overstreet and Howse (1977).

Bacterial flora including commensal and disease-causing organisms have been investigated more thoroughly than viruses. Horsley (1977) reviewed the bacterial flora of fishes and concluded that the flora in a fish's alimentary canal was about the same as that on the gills and skin, which, in turn, depended on the state of the environment. In other words, monitoring bacteria and water quality in ponds should help predict potential disease outbreaks.

The natural bacterial epizootic in the northern Gulf was first reported by Plumb, Schachte, and Gaines (1974) and later studied in more detail by Cook and Lotton (1975). Overstreet and Howse (1977) discussed some bacterial infections in Mississippi coastal areas.

A book with parts by G. Bullock, Conroy, and Snieszko (1971) and by G. Bullock (1971) deals specifically with the methods of working with bacteria from fishes. Two of several papers concerning identification of bacteria are by Glorioso, Amborski, Larkin, Amborski, and Culley (1974) and by Shotts (1976). The primary reference is *Bergey's Manual* (Buchanan and Gibbons, 1974).

Protozoans

Protozoology and even the study of parasitic protozoans represent fields unto themselves. The advances in chemistry, ultrastructure, and culturing techniques have allowed a much better understanding of the relationships among different groups. In 1964, Honigberg and a group of others formulated the committee's revised classification of the Protozoa. Since then several major changes have been suggested such as those by de Puytorac and others (1974) and Corliss (1974a; 1974b) for ciliates, and by Sprague (Bulla and Cheng, 1977) for microsporans. Several books cover protozoans in general such as those by Kudo (1966), Grell (1973), and Sleigh (1973). Levines' book (1973) specializes in parasitic forms primarily from domestic animals. Even though helpful, that book unfortunately did not treat species from fishes. The biochemistry of parasitic forms has been summarized by Gutteridge and Coombs (1977). Several papers on specific

species or groups are cited below.

Lawler (1977) has shown that all but 6 of over 80 tested fishes (different species) succumbed to heavy infestations of the dinoflagellate *Amyloodinium ocellatum*. Those six fishes usually appeared refractory to the invader. Occasionally an individual of one of those species would become infested or even die, but in those instances, another less susceptible fish was usually present. Lawler suggested the resistance of *Cyprinodon variegatus*, *Fundulus grandis*, *Opsanus beta*, and others might relate to the ability of those fish to tolerate low oxygen concentrations or to produce an abundance of mucus, either with or without a repelling substance. Lom and Lawler (1973) described the attachment mechanism of the related *Oodinium cyprinodontum* which infests gills of killifish and other cyprinodontid fishes along the Atlantic and Gulf coasts. Larger and more elongate than *Amyloodinium ocellatum*, it harbors chloroplasts. Rather than penetrating and digesting host tissue like that compared species, it attaches without harming the host and produces its own nutrients like a typical plant. That *Oodinium cyprinodontum* has such characteristics favor the host, since as many as 2000 dinospores (about eight times as many as for *Amyloodinium ocellatum*) can form from one trophont.

Several chemical treatments cited in aquarium publications as curing *Oodinium* infestations have not been successful in treating heavily-infested fish. Lawler (1977) listed several of these and emphasized the value of a short freshwater bath.

A general treatment of piscine flagellates (Becker, 1977) covered all different groups. Becker and I are presently studying some blood parasites in fishes from Mississippi, and comments on leeches as vectors for these occurred in the paper by Sawyer, Lawler, and Overstreet (1975). Dealing specifically with trypanosomes, Khan (1977) showed experimentally that at least *Trypanosoma murmanensis* in Newfoundland, Canada, infected a variety of related and non-related hosts. After being transmitted by the leech, the trypanosome continuously increased in size for about 2 months. The difference in size of blood flagellates and paucity of observations have influenced some biologists to assume that several rather specific trypanosomes occurred in some regions. Ultrastructure of stages in the leech has been investigated by Desser (1976).

Amoebae have been encountered in marine fishes. Orias and Noble (1971) listed the four reported species. All but one inhabits the alimentary tract, and it occurs in the branchial mucus and skin. None appears pathogenic to the fish, but freshwater amoebae have been implicated in mortalities, possibly in conjunction with associates (Rogers and Gaines, 1975; Sawyer, Hoffman, Hnath, and Conrad, 1975). Living individuals move about actively with their pseudopodia; in some cases they even feed on their own protective cyst stage in addition to expected food particles (W. Bullock, 1966). Critical examination of intestinal tissue and contents might reveal many amoebae in marine fishes. Based on other reports, individuals should be more prevalent when intestinal flagellates also occur, and they probably occur in clusters. Perhaps given appropriate stimulation, some of the commensal amoebae become virulent.

Several books treat coccidiosis in general (Khevsin, 1972; Levine, 1973; Hammond and Long, 1973). A brief treatment by Lom (1970) summarized much of the information about piscine species, and many new species have been described since then. Lom (1970) also treated hemogregarines and other protozoans of fish, whereas Becker (1970) confined his chapter in the same book to protozoans in fish blood. Davies and Johnston (1976) studied *Haemogregarina bigemina*, a species that reproduces asexually in peripheral blood of a blenny and other hosts; they presented strong evidence that the isopod *Gnathia maxillaris* acted as the vector. For someone interested in the fine structure and locomotion of hemogregarine gametocytes, the most observed stage in fish, Desser and Weller (1973) provided an informative paper. Olsen's (1974) book presented a diagram of a life cycle for a species utilizing a turtle and a leech, and it also gave several references for obtaining information on all stages. Generally not considered pathogenic,

hemogregarines include a species (*Haemogregarina acipenseris*) in a sturgeon from the Volga River that apparently causes anemia and wasting in its host (see Shulman and Stein, 1962).

Microsporidans have been discussed in detail in the section on crustacean hosts. The best single source of review articles and references on all aspects of the group is the two volume work edited by Bulla and Cheng (1976; 1977).

The extensive literature about myxosporidans primarily deals with spore size and shape and with hosts. Increased numbers of ultrastructural investigations on the spores and on developmental stages should enhance the knowledge of the group considerably. Kudo (1920) and Shulman (1966) wrote the classic treatments on the group, and Paul Meglitsch of Drake University has an updated monograph in progress.

Lom (1969), an active worker with myxosporidans, compared the development of the polar filament and its external tube that is drawn into the capsule with the similar process for nematocyst development in cnidarians. He used this and other features, all of which contrast with those of a microsporidan and its polar filament and with a ciliate and its extrudible organelles, to relate myxosporidans more closely with cnidarians than with other protozoans. Both groups also have dissociated generative cells.

The possession of more than one cell needs further explanation. When most disporous species develop (two spores within a membrane), ten cells form the two spores and one forms the pansporoblast chamber. For a spore, one cell forms each of the two valves and each of the two polar capsules including their contents. The nuclei of a binucleate cell often fuse to produce the infective amoeboid stage.

Pathological alterations in *Cyprinodon variegatus* (sheepshead minnow) infected with *Myxobolus lintoni* have been treated by Nigrelli and Smith (1938), Overstreet and Howse (1977), and others. Articles on trout with whirling disease probably surpass in number those on any other myxosporidan. Recently, Wolf and Markiw (1976) have artificially cultured spores from the vegetative stage. Hoffman (1974), who has conducted much research on means to control whirling disease, reported on the use of ultraviolet irradiation to control both it and a variety of other fish parasites. Treating ponds in order to control the disease is not always entirely effective (Hoffman, 1976; Hoffman and O'Grodnick 1977).

The myxosporidan cysts portrayed between the fin rays of the spot probably are referable to the same species of *Henneguya* that occurs between the soft rays of the dorsal and anal fins of the seatrouts *Cynoscion nebulosus* and *Cynoscion arenarius* in Mississippi Sound and that reported but never named from *Cynoscion regalis* in New York and Virginia by Jakowska, Nigrelli, and Alperin (1954).

Other than three species, one from an annelid, one from an insect, and one from a digenean, all reported true myxosporidans infect cold-blooded vertebrates. The pathogenic *Fabespora vermicola* from the digenean *Crassicutis archosargi* and its unusual ability to move by itself was reported by Overstreet (1976a). If the fluke harmed its sheepshead host, the myxosporidan could be considered for possible use as a biological control agent. The fluke, however, even though attaching to the intestine by an unusual adhesive mechanism (Overstreet, 1976b), apparently does not harm the fish.

References on ciliates in general were presented at the beginning of this section. By culturing a few ciliates, applying the protargol and silver impregnation techniques, maybe using an electron microscope, and exercising considerable patience, students and other scientists can still solve numerous economically and academically important problems with ciliates.

Trichodinids of marine fishes have been studied most extensively by Lom, who presented a nicely illustrated study (1973) on their adhesive disk. They have been reported to cause mortalities in marine hatcheries (*e.g.*, Purdom and Howard, 1971; Pearse, 1972), but dying fish often also harbor monogeneans, copepods, or dinoflagellates

in addition to the ciliates that may help promote their multiplication. Several species cause mortalities in freshwater aquaculture facilities. As examples (Meyer, 1970), trichodinids kill channel catfish fry within an hour after hatching and keep young golden shiners from feeding.

Red sore disease has been considered a problem for some time to people with freshwater fish-ponds (Rogers, 1972). In addition to low oxygen concentration and high organic content, other factors can promote the disease. Esch, Hazen, Dimock, and Gibbons (1976) studied the *Aeromonas-Epistylis* complex in centrarchid fishes from a cooling pond for a nuclear production facility and found that more fish from the thermally-affected region had red sores than did those from a region with water of ambient temperature. Presumably, a variety of pollutants that stress the host and encourage growth and reproduction of the ciliate and the bacterium will enhance red sore disease.

Overstreet and Howse (1977) studied the attachment of the stalk's terminal plate to host tissue and suggested that the fibrillar attachment complex of *Epistylis* sp. slowly infiltrates and erodes the host tissue leaving scale or bone as the only remaining sites on which to attach. Fish heavily infested often have exposed bones and extensive tissue destruction and regeneration. Those authors point out that hemorrhaging lesions seem to depend on the presence of scales. Catfish, without any scales, harbor dense growths of the same or similar species of *Epistylis* without much hemorrhaging even though bones may be exposed.

The major group Holotrichia no longer has acceptance in the recent classification schemes of de Puytorac and others (1974) and Corliss (1974a; 1974b). The term, however, still has some useful value in nontaxonomic works because of its long workable and familiar nature. An outbreak of *Cryptocaryon irritans* in fishes from both experimental and public aquaria was discussed by Wilkie and Gordin (1969). Hoffman, Landolt, Camper, Coats, Stookey, and Burek (1975) provided a key to "holotrichs" of freshwater fishes and discussed pathological responses by hosts, especially those resulting from *Tetrahymena corlissi*. That facultative parasite killed fish, but fish could not be experimentally infected with it.

Specimens of the sheepshead minnow from Horn Island infested with the hypotrich were collected by Adrian Lawler, and the progress of the disease was followed by the two of us (unpublished data).

Cestodes

Yamaguti (1959) compiled a book on all cestodes known at that time, providing keys to genera and higher groups. A more up-to-date set of keys was written by Schmidt (1970), but neither helps identify most larval forms. Some of these larvae from Gulf molluscs can be sorted out using a key by Cake (1976). Wardle and McCloud's (1952) book on tapeworms remains the classic for a general treatment.

Aspects of the ecology and taxonomy of the pseudophyllidean *Anantrum tortum* were presented by Overstreet (1968). Rees (1969) presented a more detailed account of several of the characters of the same worm using the junior synonym *Acompsocephalum tortum*. Before this present report, the worm had never been reported from the Gulf of Mexico, even though the worm is extremely abundant. I have confirmed that it has operculated eggs. Recently Jensen and Heckmann (1977) described a second species, *Anantrum histocephalum*, from a lizardfish in California. That worm, however, has a mushroom-shaped scolex to assure attachment within the gut epithelium.

Overstreet (1977b) reported the ecological aspects of infections of *Poecilancistrium caryophyllum* in the spotted seatrout. Moreover, Tom Mattis has been investigating the life-history of that worm and of several other elasmobranch cestodes. He is the authority from the Gulf region on elasmobranch cestodes; others that work on elasmobranch cestodes are Ronald Campbell of Southeastern Massachusetts University and Murray Dailey of California State University at Long Beach. Dailey and Overstreet (1973) described the multistrobilate forms of *Cathetocephalus thatcheri* from the bull shark.

Monogeneans

Rather than being most closely related to digeneans, monogeneans probably evolved from an ancestral form that gave rise to cestode groups. Malmberg (1974) discussed his ideas and reviewed much of the literature on monogenean phylogeny.

A book by Yamaguti (1963a) provides keys to the families and genera of monogeneans and listings of species. A more updated key for North American genera by Schell (1970) may prove more economical and up to date for a beginning student.

Many taxonomic problems still need attention, including numerous descriptions of pathogenic species. In fact, Adrian Lawler at GCRL plans to describe the new species of *Dermophthirius* that harmed its sawfish host. Lawler and Cave (1978) already reported on *Aspinatrium pogoniae* which built up infestations to thousands of individuals and apparently killed a large captive black drum. Large worms measured over 12 mm long, but most were smaller. Many species will multiply extensively in cultured fish and kill or weaken them, but few cases have been reported in the literature.

Some monogeneans that occur in Mississippi may be near the limit of their geographic range, being rare except under specific conditions. The relatively rare *Absonifibula bychowskyi* may be an example of this (Lawler and Overstreet, 1976). We found that the intensity of infestations related directly with water temperature.

The best understood monogenean infesting skin does not occur in local waters. Still, a brief understanding of the biology of *Entobdella solea* from the ventral surface of the sole should inspire extensive investigations of local species (Kearn, 1971). This 5 mm worm moves about on the bottom of the flatfish, feeding on tissue overlying scales. It lays eggs with long sticky filaments on sand grains during the day when the host is buried. Fish feed during dark hours, and about dawn they return to partially bury in the sand. At that time, a ciliated monogenean larva (onchomiracidium) hatches and infests the exposed upper head of the sole. As it matures, the worm migrates to the fish's belly. It embeds its anchors into the host, but holds on primarily by suction. Accessory hook-like structures anterior to the anchors actually prop up the central part of the holdfast making a cup. In some other species, the anchors penetrate more deeply and hold the host in a manner similar to an ice tong when the fish is active. When the fish slows down, some worms' marginal hooks suffice for attachment (Lester, 1972).

Studies by Paperna (1964) provided an understanding of infestations by more than one monogenean species in pond-reared fish. He found that heavy infestations of *Dactylogyrus vastator* on young carp caused increased growth of host tissue (hyperplasia) and created an unfavorable environment for two other monogenean species. The small worm can kill many carp fry, but fingerlings develop a resistance, so that monogenean infestations in larger fish include other less pathogenic species only. If the effect of temperature, salinity, and other physical parameters on larval and adult worms and the time when fry first appear in ponds are understood, fish can be properly managed to avoid infestations (*e.g.*, Paperna, 1963). A biologist, however, must realize that not all monogeneans' eggs have to hatch quickly; some developmentally inhibited larvae over-winter and hatch about the time young fish appear.

Another group of tiny monogeneans (gyrodactylids) produces embryos rather than eggs, and many species can coexist on the same host (*e.g.*, Williams and Rogers, 1971, for species on the sheepshead minnow). Some species cause mortalities and others inhabit atypical sites. One species even infests the brood pouch of the male Gulf pipefish (Holliman, 1963).

A large number of the marine species in the northern Gulf have been reported or described in papers by Koratha (1955a; 1955b) and Hargis (1957, for summary). Koratha (1955a) also suggested a possible phylogenetic relationship between cobia and diskfishes indicated by their monogeneans. This relationship has been questioned by several ichthyologists. Several other groups of monogeneans are also restricted to specific families or other groups of fishes. On the basis of Hargis'

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report on host-specificity, each of 67 monogeneans from the northern Gulf infested a single host species, whereas only 8 parasitized two and 1 parasitized three. When more than one host was infested, they belonged to the same genus. Similar levels of specificity to single hosts occur in the White Sea, Barents Sea, Black Sea, and Great Barrier Reef off Australia (Rohde, 1977).

Digeneans

Yamaguti (1971) revised an earlier compilation of all digeneans of vertebrates, giving keys to genera and families and listing species with their hosts. He (1975) also compiled most known data on life cycles. Both lengthy works are extensively illustrated. Shell's (1970) key allows some identifications and is much cheaper in price than Yamaguti's book, but does not include as many local marine and estuarine species.

A book by Erasmus (1972) deals with experimental investigations of trematode biology, emphasizing larval stages. Lumsden (1975) reviewed the function and structure of helminth teguments, including those of trematodes, and Overstreet (1976b) described the unusual attachment to a fish host by *Crassicutis archosargi*.

For further discussion on some of the examples presented, the reader can refer to the following works: Gibson and Bray (1977) considered the giant fish stomach worm from a variety of hosts as the single species *Hirudinella ventricosa* until further evidence confirms a second species, Iversen and Yoshida (1957) reported the common occurrence of two specimens of that giant digenean per wahoo, and Watertor (1973) discussed variations in infections of it from tunas. A general discussion on melanin-containing cells in teleosts was presented by Roberts (1975), and Dubois' (1968; 1970) synopsis covered the taxonomy and life histories of most strigeoids. Overstreet (1970; 1971a; 1971b; 1971c; 1977a) treated *Metadena spectanda*, *Saturnius maurepasi*, and the digeneans illustrated in Figures 143 to 145.

Some discussed works are still in progress. Heard and I will describe the life history of *Phagicola longus*, and I will report on ecological aspects of many parasites from the Atlantic croaker including digeneans. Courtney and Forrester (1974) reported on the worms from the brown pelican. Some heterophyids infect their intermediate hosts in large numbers. Paperna and Overstreet (in press) reported as many as 6,000 heterophyid metacercariae per gram of tissue from some mullet in the Sinai.

Even though fishes do not act as paratenic hosts for digeneans as frequently as for cestodes, nematodes, and acanthocephalans, some still function in that role. So can cephalopods (squids and related molluscs) which parallel fishes in many respects in addition to harboring the same digeneans (Overstreet and Hochberg, 1975).

For a fairly recent discussion on phylogenetic and taxonomic relationships of digeneans, readers should refer to a paper by Cable (1974). I hope Raymond Cable will share more of his knowledge about cercariae with us in the future.

Chuck Getter, a graduate student of C. Richard Robins at the University of Miami has been investigating the endangered key silverside, *Menidia conchorum*. He sent me preserved material infected with acanthostomes. Specimens of sheepshead minnow and sailfin molly also had infections. To date, only three acanthostomes have been reported from the United States, and the larva, based on the presence of 24 oral spines and other characters, appeared most like *Acanthostomum coronarium* (see Brooks and Overstreet, 1977); however, we have studied no crocodilian worms from South Florida and additional species with similar features may occur there.

Anatomical aspects of the four species of marine aspidogastrids in the northern Gulf have been treated by Hendrix and Overstreet (1977).

A review of American paragonimiasis including the pairing and encapsulation of individuals was presented by Sogandares-Bernal and Seed (1973). Literature on many marine zoonoses (parasites, including digeneans, that could infect humans and, in some cases, pets) has been synthesized by Williams and Jones (1978).

Nematodes

As he has done for other helminths, Yamaguti (1961) has compiled a listing of nematodes parasitic in vertebrates, and he included keys to genera and higher taxa. These keys, but not the listings, have been superseded by a series of keys edited by Anderson, Chabaud, and Willmott (1974a, 1974b, 1975a, 1975b). Number 1 in this series also includes a glossary which should straighten out some of the confusion among terms. A series of books in Russian have compiled much of the literature on some groups, and a few have been translated into English (*e.g.*, Skrjabin, 1949; Ivashkin, Sobolev, and Khromova, 1971). A number of other books has been written on various aspects of nematodes, and, for the present purposes, I mention those by Chitwood and Chitwood (1950) and by Bird (1971) only.

Information on the striking reddish camallanids in Gulf marine fishes has just been published (Fusco and Overstreet, 1978). *Spirocamallanus cricotus* infects shallow inshore fishes. Actually more than the 13 reported hosts can harbor infections. In water 27 meters and deeper, *Spirocamallanus halitrophus* infects at least bothid flounders and a cusk-eel. Fusco (1978b), using isoelectric focusing and spectrophotometric characterization, has differentiated hemoglobins of the Atlantic croaker, male *Spirocamallanus cricotus*, and female *Spirocamallanus cricotus*. He (1978a) also obtained experimental infections of this worm in a harpacticoid copepod (*Tigriopus californicus*) and in the white shrimp.

Adults of the common *Thynnascaris reliquens* were described by Norris and Overstreet (1975). Those authors (1976) also reported larval members of that genus in invertebrates and the ability of at least one member to invade mice. Ebert (1976) examined this latter matter in more detail. Thomas Deardorff of GCRL hopes to relate a few larval species of *Thynnascaris* with their adult forms. Much has been written about the disease anisakiasis, especially in Japan. Oshima (1972) gave a good review which has been updated by several workers (*e.g.*, Jackson, 1975; Margolis, 1977; and in progress by John Smith of the Department of Agriculture & Fisheries for Scotland, Aberdeen, Scotland).

A general treatment of nematodes in marine fishes by Margolis (1970) gave a fairly complete idea of the different major groups infecting fish. More groups than that, however, infect fish. A critical study on the life cycle of *Dioctophyma renale* by Mace and Anderson (1975) emended some of the interpretations by Karmanova (1962), who confirmed that earlier workers had indeed mistaken a gordiacean larva from the branchiobdellid from crayfish as *Dioctophyma renale*. The duck mortalities resulting from their eating fish with *Eustrongyloides* sp. were described by Locke, DeWitt, Menzie, and Kerwin (1964).

Rosenthal (1967) fed wild plankton to larval herring and many of these young fish apparently started dying from larval ascaridoid larvae after about 11 days. The worms grew rapidly and were quite active. After the fish reached 2 cm in length, they became less seriously affected by the worm. More studies of this nature should be conducted. Problems arise when using predatory fish, however, because they typically cannibalize weakened individuals. Consequently, several predatory fish cannot occupy the same aquarium and at the same time provide meaningful results.

Acanthocephalans

Yamaguti (1963b) listed the known acanthocephalans and presented keys to the higher taxa. Golvan (1969) provided descriptions and keys to the species of paleoacanthocephalans, a major group infecting fishes. Authorities do not agree about the higher classification of acanthocephalans, even though about 1000 species have been described. W. Bullock (1969) discussed the anatomy of these worms and discussed many features in relation to their use in classification and systematics. A more recent treatment on the phylum was presented by Schmidt and Roberts (1977).

One of several papers on acanthocephalans covers most of the marine fish species in the northern Gulf (W. Bullock, 1957). Buckner, Overstreet, and Heard (1978) reported intermediate hosts for

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Tegorhynchus furcatus and *Dollfusentis chandleri*, and Overstreet is preparing a several-year ecological study on the latter species in the Atlantic croaker.

Crustaceans

Kabata (1970) and Schmidt and Roberts (1977) treated many aspects of crustacean parasites. Kabata also has other books in progress which should be classics. Schultz's (1969) key can be used to identify most American isopods, and Yamaguti's (1963c) book lists and illustrates most piscine copepods.

The example discussing altered behavior of infested menhaden was by Guthrie and Kroger (1974), and that on infested and debilitated gar was by Overstreet and Howse (1977).

Life cycles of isopods on fishes need considerable attention, especially in light of the potential economic loss to cultured fish caused by isopods. A group of isopods not mentioned in the first section because members do not appear to be a problem in the northern Gulf of Mexico is the Gnathiidae. They may be a threat in south Florida. In the Red Sea, one isopod that can bring fish culture to a halt has been investigated (Paperna and Por, in press; Paperna and Overstreet, in press). The larval gnathiid (praniza), unlike the adult, obtains a blood meal from almost any fish, leaving that fish with integumentary wounds, anemic, and often dead. The larva feeds on fluid from a fish's gills or skin for about 2 to 4 hours at night and may do this three times before molting into an adult. A variety of fish species maintained in cages near shore in 1 to 2 meters of water attracted the isopod, but those in cages from deeper water of 6 to 8 meters about 100 m offshore did not. Once attacked, an individual fish rarely becomes infested again. After obtaining the blood meals, the isopod molts to an adult in about a week. Eggs develop in the female's brood pouch for about 3 weeks and then the larvae, numbering about 90 in a full-sized female, emerge. Larvae feed on fish after about 9 to 10 days of development and live in the mud in shallow habitats.

Information on life cycles of cymothoid species remains incomplete. Menzies, Bowman, and Alverson (1955) pieced together the cycle of *Livoneca convexa* on the Pacific bumper. Presumably free-swimming juveniles find the appropriate host, infest and feed on gill tissue, molt into a male, transform into a female, mate, and produce young as a commensal in the host's mouth. A similar progression does not occur for all species.

Two of the most troublesome copepod groups to identify and understand are the ergasilids and caligids. Roberts (1970) and Johnson and Rogers (1973) provided keys and data on the tiny ergasilids, and Paperna and Zwerner (1976) gave a good example of ecological aspects of an infestation of *Ergasilus labracis* on the striped bass. Margolis, Kabata, and Parker (1975) provided a catalogue and synopsis on the many species of *Caligus*, and Cressey (1967) reviewed pandarids from elasmobranchs.

Myron Loman has investigated *Lernaeenicus radiatus* in my laboratory. Using the rock seabass as an intermediate host, he obtained results similar to Shields (1970), who used the black seabass from the Atlantic coast. Copepodid larvae infest the fish, pass through a chalimus stage, mate (the male breaks its frontal filament and transfers its spermatophores to the female), leave within 3 to 5 days, infest another fish, mature, and produce eggs within a week. The Gulf killifish acted as a good final host, but readily succumbed when more than a couple of individuals infected it. Since over 100 infective larvae can infest a bass at one time, a few killifish left with a bass in an aquarium will usually die unless removed at proper intervals.

Considerable data concerning biological aspects of copepods have been gathered. Cressey and Collette (1970) provided a good example of copepod-needlefish relationships which could act as a guide for further works on other copepod-host relationships. By examining the stomach contents of remoras, sharksuckers, and other diskfish, Cressey and Lachner (1970) discovered that copepods appeared to play different roles as the food source for different diskfish. Also, age of fish determined food preferences. Young *Remora remora* ate more

parasites than older individuals, whereas older *Remora osteochir* ate more than younger fish. Bernett-Herkes (1974) found that the presence of some copepods from dolphin (fish) appeared to be influenced by size of host and by the presence of other copepod species.

Many argulids prove difficult to identify using old literature. Most likely, such problems should be solved by preliminary and future keys by Cressey (1972).

MISCELLANEOUS HOSTS

The American Alligator

The alligator harbors parasites that, for the most part, can be seen with the naked eye. Large nematodes in the stomach may be one or a combination of at least four adult ascaridoids. A new species of *Goezia* is being described by Deardorff and Overstreet, and the other three are being reviewed by John Sprent of the University of Queensland. His works will include most known crocodilian nematodes.

The most conspicuous digeneans are the acanthostomes. Sometimes hundreds of the nearly 1 cm long species inhabit a single alligator. Brooks and Overstreet (1977) described or presented supplemental data on the three known species from the United States. Other digeneans occur in lesser numbers in hosts inhabiting fresher waters. Brooks, Overstreet, and Pence (1977) reported the proterodiplostomes, and Brooks and Overstreet (1978) described the only liolopid. The digenean *Odhneriotrema incommodum* from southern Florida deserves comment because of its unusual location even though it does not infect alligators in Mississippi and Louisiana. This large worm attaches firmly to the pharynx or buccal cavity of its host, and an observer can see it by using extreme care. Its life cycle presents a good example of a parasite that infects a specific sex of host. The Florida gar (*Lepisosteus platyrhincus*), which does not occur in Mississippi, harbors the encysted metacercariae primarily in the ovary, hence a preponderance of infections in the female gar (Leigh, 1960).

By considering natural phylogenetic groups of both crocodilians and crocodilian digeneans, Brooks (dissertation in progress, University of Mississippi) presented evidence that both groups evolved together. About 200 million years ago all land masses that harbor crocodilians today were joined together as one body of land (North America, South America, Africa, Asia, and Australia). By the end of the next 50 million years, that land mass had completely broken up. Because several species of the worms belonging to the same genera occur dispersed in most regions today and because intermediate hosts of most groups cannot tolerate saltwater, the actual or ancestral digeneans appeared to already be infecting crocodilians 200 million years ago.

A stronger relationship between crocodilians and birds than between crocodilians and other reptilians is suggested by the presence of strigeoids, clinostomes, and echinostomes inhabiting both crocodilians and birds, but not other reptiles. Brooks will provide details of the association in the near future.

The presence of the turtle leech *Placobdella multilineata* on the alligator has been reported only recently (Forrester and Sawyer, 1974) and then from Florida. In Louisiana, it can be seen commonly on gators in freshwater. Just as in Florida, the hosts have a species of *Haemogregarina* in the blood which could be transmitted by that leech.

The pentastome *Sebekia oxycephala* occurs sometimes in large numbers in the lungs of alligator hosts. It also occurred in the liver and mesentery of some hosts. The alligator acquired its infections from a variety of fishes (Venard and Bangham, 1941; Dukes, Shealey, and Rogers, 1971). Self (1969) presented a review and bibliography of pentastomes in general.

Birds

Symbionts and diseases of birds have been treated extensively in a book edited by Davis, Anderson, Karstad, and Trainer (1971). Another general book by Rothschild and Clay (1957) placed more emphasis on

the arthropods. In order to appreciate the wealth of information available on the helminths of just the Anatidae, one can inspect the bibliography and catalogue by McDonald (1969a; 1969b). Sources to identify helminths are basically the same as for helminths infecting fishes.

Marine and estuarine fish play an important role in transmitting helminths to birds. As already shown earlier, they readily transmit numerous digeneans and nematodes to birds. To a lesser extent, these fishes transmit cestodes, acanthocephalans, and other helminths. As an example, killifishes can be cited for hosting cestodes belonging to the genus *Parvitaenia* which infect ibis, herons, pelicans, and other birds as determined by Richard Heard (personal communication) and the roughly 5 cm long acanthocephalan *Arhythmorhynchus frassoni* which infects the clapper rail (Nickol and Heard, 1970).

Much information known about parasites of local birds has been reported by Danny Pence of Texas Tech University who studied the numerous nasal mites from Louisiana birds (Pence, 1973b; 1975). In addition to those parasites, he reported on a variety of worms that have importance for different reasons. As examples, the digenean *Amphimerus elongatus* occurred in the thousands in the bile ducts of the double-crested cormorant, causing extensive cirrhosis and other pathological alterations (Pense and Childs, 1972), and the nematode *Tetrameres aspinosa* encysted in pairs in the proventriculus of the snowy egret (Pence, 1973c). Nothing was particularly notable about that tetramerid infection except that anyone examining the proventriculus and stomach of any birds should be aware of the presence of those encysting nematodes. The embedded blood-red female, rather than looking nematode-like, is extended greatly about the midbody. Either the males occur encysted with the females in fibrous cysts or free in the stomach or proventriculus, depending on the species. The conspicuous cysts with red worms can be seen through host tissue, appearing at first glance like hemorrhagic lesions. An extensive review of the group is in preparation by Tony Mollhagen (1977, abstract) working under the direction of Pence.

Pence (1973a) reported the pentastome *Reighardia sternae* from gulls and terns in Louisiana. It also infects the lungs and air sacs of at least the laughing gull and common tern in Ocean Springs. Rather unique in that it infects birds, it may also be unusual in not requiring an intermediate host (Riley, 1972a). However, like the species in the alligator, *Reighardia sternae* may also be transmitted by fishes (Bakke, 1972). Those interested in the variety of feeding mechanisms that parasites use to ingest host blood should consult papers by Riley (1972b; 1973) who reported observations and described the method used by this pentastome.

In order to identify and study arthropods, a reader could initiate his literature search using publications by Emerson (1972a; 1972b; 1972c) for lice, Cooley and Kohls (1945) for ticks, Pence (1972) for subcutaneous hypopial mites, and Pence (1975) for nasal mites. The reference to the bloody ulcers produced by a louse in the mouth of the white pelican was by Wobeser, Johnson, and Acompanado (1974) and that to the possible evolutionary history of flamingo-lice was by Rothschild and Clay (1957).

This latter relationship among the flamingos and other groups remains unsettled. Osteological evidence based on a combination of characters of fossil flamingolike waders from the Lower Eocene supports the relationship of flamingos with anseriforms (ducks) and also with charadriiforms (shorebirds) (Feduccia, 1976). In fact, similarities in cestodes occur between flamingos and shorebirds (Baer, 1957). However, the consensus of most present-day ornithologists (Oscar T. Owre, personal communication) supports Sibley and Ahlquist (1972) who believe that flamingos, while related to ducks, align closer with Ciconiiformes (herons), and that, as suggested by Mayer and von Keler (see review by Sibley and Ahlquist), the lice transferred recently from waterfowl to flamingos. As possible tools to help solve the problem, the affinities of quill mites (syringophilids) and nasal mites (dermanyssids) from flamingos should be investigated.

Some important protozoans, bacteria, and viruses of wild birds have been treated in some detail by Davis, Anderson, Karstad, and Trainer (1971). Levine (1973) covered many more protozoans, including *Sarcocystis rileyi*.

Marine Mammals

Marine mammalian parasites have been described in a book (Delyamure, 1955) and compiled into a checklist (Dailey and Brownell, 1972) in another book that provides a wide range of diverse information on these mammals (Ridgway, 1972). An annotated treatment of porpoise parasites (Zam, Caldwell, and Caldwell, 1971) supplements a review on this host's common diseases encountered by veterinarians (Sweeney and Ridgway, 1975). Lowery (1974) discussed marine mammals in the northern Gulf. Gunter and Overstreet (1974) reported parasites from a dwarf sperm whale in Mississippi Sound, and I have seen all the dolphin parasites discussed earlier in hosts from Mississippi. David Gibson and Rod Bray have designed a display of the large species of *Crassicauda* for the British Museum (Natural History).

The possible role of campulids in single strandings was suggested by Ridgway and Dailey (1972). Perhaps multiple strandings could result from a dominant leader being affected by parasites and the subordinates following that leader to beach themselves regardless of the consequences. Other parasites also have the potential to interfere with the "sonar" system in these animals.

MISCELLANEOUS SYMBIONTS

A review of the mermithids was presented by Nickle (1972). Petersen (1973) is one of several who have reported on the use of these nematodes in controlling mosquito populations. Presently, one species, *Reesimermis nielseni*, has been especially fruitful for this purpose. It feeds on the hemolymph of and kills over 20 species of mosquitoes. The larva can successfully infect a large percentage of a mosquito population. Since the worm does not feed after it leaves its host-mosquito, it can be handled easily, and the preparasitic juvenile can be reared and collected in large numbers. Preliminary field applications of 1000 larvae per square meter killed most of the mosquitoes, and the worm became permanently established in some of the sites (Petersen and Willis, 1972).

The illustrated midge with the mermithid came from Simmon's Bayou near Ocean Springs when the salinity was 6 ppt (14 April 1977) and the associated animals consisted primarily of estuarine species.

A classic work on nematomorphs by May (1919) described the life histories of two species, and both Pennak (1953) and Cheng (1973) provided a general treatment of the group. Born (1967) reported *Nectonema agile* from the grass shrimp.

The leech *Stibarobdella macrothela* was recently treated by Sawyer, Lawler, and Overstreet (1975) and by Penner and Raj (1977). A few turbellarians were discussed as symbionts of oysters; Jennings (1974) discussed many more and showed progressive stages from totally free-living to parasitic.

Barnacles from bands on the dusky shark were collected by Tom Mattis while in search of elusive tapeworms. William A. Newman of Scripps Institution of Oceanography identified *Conchoderma auritum* and Cindy van Duyne of North Central College in Naperville, Illinois, identified the other two. According to Newman (personal communication), *Conchoderma auritum* usually attaches to sessile barnacles on whales, but sometimes occurs on baleen or on the teeth of toothed cetaceans when their lips are damaged. Newman got one off a submarine. Dawson (1969) previously reported the only record of *Conchoderma virgatum* from the Gulf of Mexico and listed cases in other parts of the world where the organism attached directly to fishes and to parasitic copepods. Unexpectedly, all hosts are not those that bask or remain in surface water where one might consider the barnacle's larvae most able to infest hosts.

Biting gnats (*Culicoides* spp.) that occur in the northern Gulf have been studied from several localities, and their activities differ some from place to place (Khalaf, 1967,

1969; Kline and Axtell, 1976). Because there was a dense population of *Culicoides hollensis* last fall (1977) and because the weather has been so nice during the early weeks of this spring, the present population of gnats has me satisfied being inside writing this booklet rather than being outside.

According to Robert C. Lowrie, Jr. (personal communication, Delta Primate Center), our populations of gnats have not been implicated in transmitting viruses nor hosting any local filarid nematodes. Lowrie has examined many individuals and never seen natural filarial infections; however, he found local gnats to experimentally support some exotic filaria.

FISH-KILLS AND MISCELLANEOUS DISEASES

Often a fish-kill results from a combination of factors. Comments on the physiology of fish related to a cold-kill were treated by Overstreet (1974). Gunter (1941) and Moore (1976) are two of several who have reported on fishes killed by the cold in Texas where such mortalities occur more frequently than in Mississippi. May (1973) reported on the occurrence of jubilees in Mobile Bay and how the first account was in 1867 even though he searched documents dating back to 1821 which should have mentioned early periodic fish-kills if they had been present. According to May, the reason for the increasing frequency of jubilees appears to be the decreasing ability for the water of Mobile Bay to transport, deposit, dilute, and assimilate the amount of organic matter in the bottom water. Most of the matter comes from natural sources of wood and leaves, but is supplemented by the increased amount of domestic wastes.

The jubilees in Mississippi, according to Charles Lyles (personal communication, Gulf States Marine Fisheries Commission), and possibly those in Alabama, too, result from plankton blooms. Lyles has observed many jubilees along Bellefontaine Beach since the late 1930's and found several items common to all. They occur during neap tides (tides with smallest differences between high and low tide occurring after the first and last quarters of the moon) at night between late June and early September. Usually rain precedes them, and the well-defined affected water has a tea color. Apparently the proper nutrients allow succession of a phytoplankter that might produce a similar toxin to that of dinoflagellate blooms of a red tide or a condition that otherwise creates an unhealthy water mass. These jubilees certainly demand critical investigation!

Numerous papers deal with red tide. Not until recently, however, has anyone critically examined dead and dying animals. Quick and Henderson (1974, 1975) report such findings, and Forrester and others (1977) go into more detail and speculation concerning an epizootic affecting lesser scaup.

Sources of pollution are being examined more extensively in recent years because of an increased concern for the environment. Overstreet and Howse (1977) briefly reviewed pesticides, heavy metals, and other sources of pollution and possible stress-related diseases in Mississippi estuaries. Pollution-sources from other regions have also been documented (*e.g.*, Alabama by Crance, 1971). More extensive studies have dealt with potential and actual problems in Chesapeake Bay (McErlean, Kerby, and Wass, 1972). Sindermann (personal communication) is preparing a review of various diseases associated with aquatic pollution.

Deaths and disease in the natural marine environment are hard to document and the causes even harder to determine. Usually a combination of factors act together. One of those factors is often temperature. Some fish, especially pelagic ones, swim faster when the temperature is either raised or decreased under experimental conditions (Olla, Studholme, Bejda, Samet, and Martin, 1975). Increases in localized water temperatures are rapidly becoming normal biproducts of modern technology (*e.g.*, Cairns, 1972). Primarily because of power plants, critical research has been conducted on the effects of fish by increased temperature combined with chlorine (Meldrin,

Gift, and Petrosky, 1974) and with other chemicals (Cairns, Health, and Parker, 1975).

In addition to natural mortalities caused by a rapid drop in temperature, mortalities can also result from sudden rainfall and storms. Dawson (1965) documented deaths of the lancelet (*Branchiostoma caribaeum*) in Mississippi following heavy rains with a subsequent drop in salinity. Most likely other animals also die under such adverse conditions. Storms can kill fish, especially transient species not normally occupying shallow inshore regions (Robins, 1957). The fishes accumulate sediment in their gill chambers, and their gills fray. Regular inhabitants of shallow, wind-exposed regions appear capable of withstanding considerable turbulence.

Human activities have now stressed the environment to a greater degree than corresponding means have been designed to protect that environment. Our wastes and other activities are taking their toll on the environment. Unfortunately, only when fish die in large numbers do people worry about the problems. Would many people be concerned about dumping sewage sludge in the New York Bight had not there been an extensive kill (Bullock, 1976)? Dredging, bulkheading, and filling in natural marshes seldom cause extensive fish-kills, but those activities nevertheless decrease numbers of animals (*e.g.*, Trent, Pullen, Proctor, 1976). Even flushing detergents into our waters has serious effects (Abel, 1974), but these effects seldom meet public view. Man needs sounder management programs, and perhaps these should be oriented toward protecting important ecosystems rather than protecting specific species. Cairns (1975) commented on this strategy and on the fact that our actions do not match our public statements. In order for substantial changes to occur, the life styles of people must also change.

As pointed out several times, the most important factor in transforming an infection into a disease is stress. A readable book by Wedemeyer, Meyer, and Smith (1976) on this problem provides a valuable background in regard to fishes.

A recent compilation of contributions on genetics and mutagenesis of fishes goes into considerable detail on many aspects of genetics (Schröder, 1973). Investigations into chromosomal anomalies in marine fishes have been recent and very fruitful (Longwell, 1976). Apparently Longwell's methods of detecting anomalies allow evaluation of material from museum collections and thereby a means of comparing collections from past years when the water was relatively clean with those collected recently from the same regions after water-quality had deteriorated. She (personal communication) has been compiling much more extensive data that corroborate her earlier findings.

Nutrition of fish has been covered in detail in a book edited by Halver (1972), and that book gave a number of examples and references which should guide any student interested in different aspects of nutrition. Examples of scoliosis (spinal column twisted in a sideways direction) such as that shown for the striped mullet (*Mugil cephalus*) as well as cases of lordosis (spinal curvature tending toward a vertical direction) are presented. Diets deficient in tryptophan or ascorbic acid produce both conditions experimentally as does a lack of calcium phosphate or an infection with a few different bacteria and parasites. Another book (Neuhaus and Halver, 1969) also covered nutrition, metabolism, genetics, and cancer. Representatives of most tumors from fishes that have been studied scientifically have been deposited in the "Registry of Tumors in Lower Animals" at the National Museum of Natural History. John Harshbarger, who directs that registry and identifies most of the neoplasms, has published extensively on the available material (*e.g.*, 1977). That paper occurs with several others in a volume on "Aquatic Pollutants and Biological Effects with Emphasis on Neoplasia" (Kraybill, Dawe, Harshbarger, and Tardiff, 1977). Edwards and Overstreet (1976) reported on the neoplasms in the striped mullet, and Overstreet and Edwards (1976) also reported benign fibromas in the southern flounder and sea catfish and reviewed the observations of other tumors from the northern Gulf.

That many tumors and other diseases are caused by environmental contaminants is based almost entirely on circumstantial evidence. Aquatic examples have been documented primarily from freshwater habitats because such habitats are often excessively polluted and because specimens are easier to collect from these confined regions than from open marine and estuarine ones. Edwards and Overstreet (1976) suspected the tumor on mullet might result from pollutants. Mearns and Sherwood (1976) also considered this possibility for skin tumors in a southern California flatfish, but did not think improvements in municipal waste treatments would reduce the prevalence of tumors unless the improvements increased the number of young fish. They (Sherwood and Mearns, 1977), however, presented strong observational and experimental evidence linking chlorinated hydrocarbon pollutants (*e.g.*, DDT) with fin-erosion in the same flatfish exposed to the discharged municipal waste water.

Many examples of injuries that cause anomalies have been indexed in the bibliographies by Dawson (1964; 1966; 1971) and Dawson and Heal (1976). Bird (1978) reported straps encircling carcharhinid sharks, including a postscript on the affected dusky sharks mentioned in the present treatment of barnacle symbionts. The Atlantic croaker with its rubber band was reported by Oversteet and Lyles (1974). Even though a few fishermen may deliberately place a band about a fish as a joke, most fish ring themselves naturally. Lamont (1961) pointed out the abundance of mackerel ringed with contraceptives occurring near sewage effluents.

Dawson's bibliographies cited references to all types of anomalies, including those of flatfish. According to the literature, reversal in *Eutropus crossotus* is rare. Taylor, Stickney, and Heard (1973) reported the first case from Georgia, and James Ray Warren in the Fisheries Section at the Gulf Coast Research Laboratory, who found the specimen photographed above in Back Bay of Biloxi has found only one other example of a reversed fringed flounder, and it occurred in a pass off Horn Island. Dawson (1962) and Moore and Posey (1974) described and reviewed many abnormalities in the hogchoker. Norman (1934) and Gudger (1934) laid the foundation for discussing anomalies in flatfishes, and that foundation continues to be built upon today.

Est ut omne hoc vobīs stercus sit,
sed mihi panis et butyrum est.

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GLOSSARY

The following definitions are included to aid those not familiar with technical terms. One desiring more information on specific terms dealing with parasites should refer to one of the cited works or some other treatment of the group in question. Too large a number of vertebrate and invertebrate host-groups are mentioned in the text to discuss or classify here; therefore, a reader wanting more information on a host should examine an encyclopedia, a book on the general group in question, or specific papers, several of which have been cited in the text.

apron of crab - The thin abdomen which is folded forward on the crab's underside; it is sometimes called the tail.

benthic - Living in, living on, or referring to the bottom.

carapace - The hard outer protective covering of some animals. In crustaceans, it covers the head and gill region.

chitin - A skeletal material of arthropods and other invertebrates that decomposes to specific chemicals (glucosamine and acetic acid), if boiled with concentrated hydrochloric acid. When impregnated with calcium salts, it may help form a firm exoskeleton.

chlorophyll - Any of several pigments capable of photosynthesis. They provide the green and yellow colors of many plants.

chloroplast - The structure containing chlorophyll embedded in a cell.

chromatophore - A pigment-containing cell that by expansion or contraction can change the overall color of an organism.

community (biotic) - The group of species of plants and animals living in and characteristic of a given habitat.

cuticle - The noncellular (therefore nonliving), usually horny, protective outer covering of many invertebrates produced by the animal.

disease - An abnormal condition of an organism or part that impairs normal physiological functioning.

estuary - The brackish water regions of and near river mouths influenced by tides.

fibroblast - A connective-tissue cell that can produce collagen, the primary component of scar tissue.

fish/fishes - "Fish" may be singular for a species or an individual or plural when referring to more than one individual of one or more species. "Fishes" is used when referring to two or more species, disregarding the number of individuals. The term for a group of individuals comprising a variety of species used herein is "fish," but some ichthyologists prefer the term "fishes."

free-living - An organism or stage not symbiotic with a host; the organism may be parasitic during one stage in its life history and free-living in another.

gamete - The mature sperm or ovum capable of participating in fertilization.

hemoglobin - One of several pigments used to transport oxygen, consisting of an iron-complex coupled to a protein. It occurs in the red blood cells of most vertebrates and in body fluids or corpuscles of a variety of nonrelated invertebrates.

hemolymph/hemocytes - Hemolymph is the circulatory fluid that bathes tissues of some invertebrates that do not have the closed circulatory system found in vertebrates. It is functionally comparable to blood and lymph of vertebrates. The blood cells are called hemocytes.

host-specificity - The degree to which a parasite can mature in more than one host species. If a parasite infects only a single species, it is highly host-specific.

humoral-cellular mechanisms - When referring to immunity, responses are both blood-mediated (humoral) and cell-mediated. Antigenic responses involve both systems.

hyaline - Refers to being translucent or transparent without the presence of fibers or granules.

hyperparasite - An organism which parasitizes another parasite.

hypha/mycelium - The mycelium is the vegetative filamentous stage of a fungus, and an individual branch is called a hypha.

inclusion body - A particulate body found in cells of tissue infected with a virus.

infection/infestation - An infection is the invasion or state resulting from an invasion by a parasite or a pathogen into a host. An infestation is an external rather than internal invasion. If both internal and external organisms occur on one host, all the associations are collectively referred to as infections. Some biologists, however, restrict the term "infestation" to either internal or external associations with metazoans. Neither an infection nor an infestation necessarily implies disease.

instar - A larval stage of an insect characterized by the animal's size and form between molts.

intermediate host - A host in which a larval parasite develops, but not to sexual maturity.

long-line - A fishing line usually maintained by an anchor and buoy with numerous, spaced, hooked lines.

lorica - A secreted noncellular (therefore non-living) protective case. The examples in the text all involve ciliate protozoans.

measurements - For those confused about metric units, the following aids might help.

	multiplied by the following number is	
centimeters	0.3937	inches
inches	2.54	centimeters
feet	30.48	centimeters

liters	0.2642	gallons
gallons	3.785	liters

1 meter = 100 centimeters (cm) = 39.37 inches

1 cm = 10 millimeters (mm) = 0.394 inches

1 mm = 1000 microns (μ) = 0.039 inches

The diameter of a human headhair varies among individuals; those of a few friends range from 60 to 80 μ wide.

A common wooden pencil is about 7 mm (5/32 inch) wide.

A penny is 19 mm wide by about 1 mm thick.

A stick of gum is 75 mm (7.5 cm or about 3 inches) long.

A 10 ounce (about 0.3 liter) Coca-Cola bottle is 24.5 cm (9 21/32 inches) high.

metabolic - Pertaining to the complex of physical and chemical processes involved in maintaining life.

necrotic - Refers to the pathologic death of living tissue while still on a living body as opposed to that which continually dies and is sloughed.

niche - The position or status of an organism within its community resulting from structural adaptations, physiological responses, and innate or learned behavior.

photosynthesis - The synthesis of simple organic matter from carbon dioxide and water, using light as the energy source.

phylogenetic - Referring to the evolutionary development of a plant or animal.

phylum (pl. -la) - A primary taxonomic division of the animal (or plant) kingdom. As an example, snails, clams, chitons, and octopus all belong to different classes in the phylum Mollusca.

plankton - The floating and drifting aquatic organisms whose primary movements result from water movement rather than their swimming efforts.

prepatent period - That period between invasion by a disease-agent and demonstration of disease or a parasite in the body (such as by eggs or cysts in feces).

prevalence/incidence - Prevalence is the degree to which a disease or infective agent occurs. It is often measured as the percentage of a population affected with a particular organism at a given time. Many biologists define incidence identically. More precisely, the term "incidence" indicates the rate of occurrence of new cases of a particular infection in a population.

reservoir host - An organism serving as a source of infection for a specific organism by harboring the infectious agent.

resistance - The ability of an organism to withstand the effects of physical, chemical, and biological agents which might otherwise debilitate it.

salinity - The sum of the various salt components in seawater usually represented as parts per thousand (ppt). Open ocean salinities remain about 35 ppt (3.5% salt), and in Mississippi Sound, salinity values usually range between 6 and 15 ppt depending primarily on the direction and force of the wind.

sclerotized - Hardened by substances other than chitin.

serum/plasma - Plasma is the watery fluid containing salts, proteins, and other organic compounds in which blood cells are suspended. After the blood clots and loses many constituents, the clear remaining fluid is serum.

sign/symptom - A sign is any objective evidence of a disease or disorder, as opposed to a symptom, which is the subjective complaint of a patient.

sp. - Abbreviation for species, and when used in conjunction with a generic name, it indicates the identification of the species is unknown or uncertain. If more than one species of a genus is being referred to, *spp.* is used.

spent - Referred to in above context as depleted of most reproductive products.

spore - A term defining a different structure for different organisms. Typically a single - or few-celled resting or resistant stage produced asexually.

substrate substratum (pls. -tes, -ta) - A substrate is the material or substance upon which a chemical enzyme acts, whereas a substratum is the underlying material on which an organism grows or attaches.

systemic - Pertaining to the entire body, such as an infection with a bacterium dispersed through the body by the blood stream.

tumor cancer - "Tumor" refers to a swelling serving no physiological function; it may be a neoplasm, a parasitic outgrowth, or any other growth. A neoplasm may be benign or malignant, the latter being characterized by its ability to invade tissue and metastasize to new sites. Typically, only a malignant neoplasm is referred to as a cancer.

vector - An invertebrate or in some cases wind, water, or other agents which transmit a parasite or disease organism, usually to a vertebrate recipient. If development of a parasite occurs, the host is called an intermediate host unless development includes sexual reproduction and then it is called an invertebrate host. Man is actually the intermediate host for malaria organisms which have their sexual stage in mosquitoes.

zooid - An individual forming part of a colony in the Protozoa, Cnidaria, and other groups. A zooid can specialize in reproduction, feeding, food capture, protection, or locomotion.

zoonosis - A disease of invertebrates or vertebrates other than man which may be transmitted to man.